

Systematics, Osteology and Phylogenetic
Relationships of Fishes of the
Ostariophysan Subfamily Anostominae
(Characoidei, Anostomidae)

Richard Winterbottom



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Systematics, Osteology and Phylogenetic Relationships of Fishes of the Ostariophysan Subfamily Anostominae (Characoidei, Anostomidae)

Abstract

The systematics of the South American characoid subfamily Anostominae is reviewed on the basis of 36 morphometric and meristic characters, and the osteology is described. A new genus, *Pseudanos*, is described for a monophyletic lineage previously assigned to *Anostomus*. Two new species, *Anostomus intermedius* and *Pseudanos irinae*, are described. The subfamily consists of five genera, three of which are monotypic. A hypothesis of the phylogenetic relationships of the members of the Anostominae is presented, based primarily on their osteology. The monotypic genera together form a monophyletic assemblage. Zoogeographic interpretations are not attempted, since vast areas (particularly in the central Amazon basin) are as yet either not or inadequately sampled. Considerable distributional extensions and discovery of new forms are to be expected in the future.

Abstracto

La sistemática de los Characoides Sud-Americanos (Caracoides), subfamilia Anostominae es revisada en base a 36 caracteres morfométricos y merísticos, describiendo también su osteología. Un nuevo género, *Pseudanos* es descrito en un lineage monofilético, anteriormente asignado a *Anostomus*. Dos nuevas especies son descritas: *Anostomus intermedius* y *Pseudanos irinae*. La subfamilia consiste de cinco géneros, tres de los cuales son monotípicos. Se presentó una hipótesis de la relación filética de los Anostominae, basada principalmente en su osteología. Los géneros monotípicos forman en conjunto un grupo monofilético. Interpretaciones zoogeográficas no son intentadas, ya que regiones muy vastas (especialmente en la Cuenca Central del Amazona) no han sido aún, o solo parcialmente estudiadas. Una distribución extensional mucho mayor y el descubrimiento de nuevas formas se esperan en el futuro.

Introduction

The hierarchical rank of the South American characoids here recognized as comprising the family Anostomidae has fluctuated like most of the suprageneric groupings among these fishes. I follow Greenwood et al. (1966) and Lindberg (1974) in elevating the subfamily Anostominae of Myers (1950) and Géry (1961) to family status. The closest relatives of this assemblage may lie among the chilodontid fishes (Roberts, 1969:424), the two families sharing unique characters (for characoids) such as the posteriorly replaced and cusped pharyngeal teeth. Géry (1961) did not mention chilodontids as possible relatives of his Anostominae, but his dendrogram does include curimatids, prochilodontids, erythrinids, lebiasinids and hemiodontids. Cockerell (1914) placed *Anostomus* in his Hemiodinae (while retaining, for some reason, the Anostomatinae for *Leporinus*), and stated that the scale structure of the two genera was very similar.

Although this paper is not concerned with the relationships of the entire family Anostomidae, I propose a new concept for the subfamily Anostominae (here conceived as encompassing the genera *Anostomus*, *Pseudanos*, *Gnathodolus*, *Sartor* and *Synaptolaemus*) on the basis of its monophyly (see the diagnosis of the subfamily, p. 4, and discussion, p. 48).

Other genera I recognize in the family Anostomidae (but here exclude from the Anostominae) are *Abramites*, *Anostomoides*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytiodus* and *Schizodon*, following Myers (1950) and Géry (1961, 1972/73). This number will probably be increased when further specimens make it possible to describe formally an anostomid with more than 65 lateral line scales from the vicinity of Manaus figured and described (but not named) by Géry (1972/73), and another form from the Essequibo River which has an incomplete lateral line (and is represented by three small specimens in the collections of the National Museum of Canada).

After this paper had been accepted for publication, I received a copy of Géry's (1977) "Characoids of the world". In this work, Géry recognizes the family Anostomidae, and includes all the genera accepted here. However, we differ significantly in subsequent subdivision. Géry (op. cit.) recognizes a subfamily for *Leporellus* (Leporellinae), and includes all other genera in his subfamily Anostominae. He gives two characters to justify this decision, but both would appear to be autapomorphies of *Leporellus* (nostrils close together, caudal fin scaly). Perhaps more importantly, Géry includes *Laemolyta* as a subgenus of *Anostomus*, while continuing to recognize the monotypic genera (*Gnathodolus*, *Sartor* and *Synaptolaemus*) as distinct. The evidence presented by Géry appears to be based on suggestions that *Laemolyta* shows a more or less intermediate condition in mouth position, nature of the teeth, and head-standing proclivities between *Anostomus* and the more generalized anostomids. While this may be true, it does not justify the inclusion of *Laemolyta* in *Anostomus* in terms of phylogenetic reasoning. Thus it is not surprising that Géry's conclusion is not supported by the results of this investigation—indeed, *Anostomus* (*Anostomus*) as conceived by Géry is itself a paraphyletic group. It may be, however, that *Laemolyta* represents the sister group of the Anostominae as here conceived (implying that the non-anostomine anostomids are not monophyletic), but this possibility must await further investigation.

Géry's (1977) book is of considerable interest for the colour photographs of six species of anostomines, most of them by Harald Schultz. Among these are *Synaptolaemus*, *Sartor* and, probably, the new species of *Anostomus* described in this paper. Schultz collected the specimens of the latter from Brazil's Xingu River—the caption of the plate is “*Anostomus (Anostomus) plicatus*” a species which is restricted to the Essequibo River System of Guyana. I have not seen any specimens of the true *A. plicatus* that have been collected by Schultz, and I suspect the plate is of the new species from the Xingu.

The subfamily is more or less restricted to the Amazon basin (exclusive of the Rio Negro, although a few small specimens, usually of *P. gracilis* and *P. trimaculatus*, have been collected in the Rio Negro near Manaus), the Orinoco, and the eastward flowing rivers of the Guyanas and Surinam. Such information as exists on the habitat of these fishes indicates a fairly broad spectrum ranging from small streams to relatively large rivers. The genera *Anostomus* and *Pseudanos* appear to be predominantly herbivorous, although occasionally taking insects and their larvae in large numbers (Winterbottom, 1974a). Weitzman (pers. comm.) has observed about 20 specimens of *A. anostomus* picking mucus off an Australian lungfish in an aquarium. An aquarium specimen of *Gnathodolus* has been observed to remove scales from its tank mates (G. Howes, pers. comm.), a possible function of the greatly enlarged symphyseal lower jaw teeth of this species.

One of the difficulties commonly encountered by ichthyologists studying South American fishes is the paucity of comprehensive collections from almost the entire area. (A notable exception is the extensive material collected by Nijssen and Boeseman in Surinam.) As a result, it is often all but impossible to discover whether two apparently different forms are linked by continuous but as yet unsampled populations or represent different species. The problem is particularly apparent among anostomines in the *P. trimaculatus* species complex.

A characteristic of all anostomines so far observed alive is their proclivity to adopt a near vertical, head down position in the water. Quite what, if any, the relationship of this position has to the upturned mouth of these fishes has not, to my knowledge, been investigated. Since Knöppel's (1972) work indicates that most of the species of this subfamily are herbivores/detritovores, I find it difficult to envisage a causal relationship between mouth position and head standing.

Materials and Methods

Specimens from many museums (see Appendix I and Acknowledgements) were measured with dial calipers to the nearest tenth of a millimeter. The method of counting and measurement follows Winterbottom (1974a). See Figure 1. A total of 36 characters was taken from each specimen. Two computer programs were used to process the data, one to transform the morphometric data to percentages, and print out the mean, range, standard deviation and standard error. This program also drew up Hubbs-Hubbs diagrams and performed an analysis of variance. The second program drew the graphs and the regression line. The coefficient of determination (R^2) was

calculated by the following formula (taken from the Hewlett-Packard HP-25 Applications Programs, 1975). The assumption is made that the relationship between variables is linear (which is not always true).

$$R^2 = \frac{\left[\sum xy - \frac{\sum x \sum y}{n} \right]^2}{\left[\sum x^2 - \frac{(\sum x)^2}{n} \right] \left[\sum y^2 - \frac{(\sum y)^2}{n} \right]}$$

The synonymies given in the systematic section of this paper are selective, ignoring for the most part the scattered and often inaccurate aquarium literature.

Skull proportions taken from cleared and stained material are measured as follows: length—anterior tip of ethmoid to basioccipital condyle; width—between hyoman-dibular fossae where sutures of prootic, pterotic and sphenotic meet.

Systematic Section

Subfamily Anostominae (new concept)

Diagnosis

South American characoids with a supra-terminal (i.e. dorsally opening) mouth, four teeth in each half of upper jaw and one to four teeth in each half of lower jaw. Apart from abnormal individuals, dorsal fin always iii 10 or iv 9, anal iii 8 or iv 8, dorsal transverse scales 3½–6, ventral transverse 3–5, 12 or 16 circumpeduncular scales, 37–45 lateral line scales and 35–42 vertebrae (excluding ural centrum). Gill membranes usually fused to isthmus. Metapterygoid/quadrate fenestra very much reduced, or absent, dorsal portion of metapterygoid either sloping medially or horizontal. Median ethmoid always longer than wide, no rhinosphenoid, parasphenoid with a vertical flange or lamina of bone. Last ray of dorsal and anal fin split to base, adipose fin present. Dorsal and pelvic fins inserted at about middle of body, head length 22–33 per cent SL. Figure 2 shows Hubbs-Hubbs diagrams for lateral-line scales of anostomines. Table 1 presents the mean and ranges of the Anostominae for selected body proportions, lateral-line scales and vertebrae.

Artificial Key to the Genera and Species of the Anostominae

- 1. Symphyseal (medial) teeth of lower jaw essentially same size as those next (lateral) to them; lower jaw (bone without teeth) as long as wide; lips without dermal papillae (may be corrugated)4
Symphyseal (medial) teeth of lower jaw enlarged; lower jaw (bone without teeth) longer than wide; lips with distinct dermal papillae2
- 2. Circumpeduncular scales 16, head depth 80–90 per cent of head length; a single tooth in each half of lower jaw (Orinoco/Casiquiare bifurcation) *Gnathodolus bidens*
Circumpeduncular scales 12, head depth less than 80 per cent of head length; 3 to 4 teeth in lower jaw3
- 3. Lower jaw about five times as long as wide, inclined posterodorsally when mouth fully closed; three teeth in lower jaw, symphyseal pair being five times as high as wide and projecting above upper jaw when mouth closed (upper Xingu) *Sartor respectus*
Lower jaw about twice as long as wide, vertical when mouth fully closed; four teeth in lower jaw, symphyseal teeth about twice as high as wide (Orinoco system and upper Xingu) *Synaptolaemus cingulatus*
- 4. Colour pattern of more than one dark longitudinal stripe greater than one scale wide on a pale background5

Colour pattern without longitudinal stripes greater than one scale wide; with two to four dark blotches or spots along lateral line (except in some individuals or *P. gracilis* where a single stripe centred on lateral line may be present, and no dark blotches present)7
- 5. Three branchiostegal rays, a median light longitudinal stripe along predorsal region, rows of light spots on anterior dorsum (south-eastern Amazon tributaries, Orinoco system and drainages south of this to Surinam) *Anostomus ternetzi*
Four branchiostegal rays (first ray may be much reduced); a median dark longitudinal stripe along predorsal region, no spots6
- 6. Greatest body depth 27.5–29.5 (\bar{x} = 27.9) per cent SL; depth of head 78–85 (\bar{x} = 81.4) per cent head length; 12 caudal vertebrae (including ural centrum and vertebra of haemal spine which lies just anterior to first anal pterygiophore) (French Guiana) .. *Anostomus brevior*
Greatest body depth 16.0–28.5 (\bar{x} = 22.6) per cent SL; depth of head 49.5–80.0 (\bar{x} = 66.2) per cent head length; usually 11 caudal vertebrae (12–13 rarely) (Amazon and Orinoco systems and drainages south of the Orinoco to Surinam) *Anostomus anostomus*

7. Four branchiostegal rays; symphyseal teeth of lower jaw truncate in specimens of 60 mm SL and larger; distance from snout to pelvic fin origin greater than distance from dorsal fin origin to caudal fin origin8
- Three branchiostegal rays; symphyseal teeth bicuspid (occasionally truncate from wear in large specimens >80 mm SL); distance from snout to pelvic origin equal to or less than distance from dorsal fin origin to caudal fin origin10
8. Snout length 40 per cent of head length; vertical pigmented areas absent below lateral line (Upper Xingu) *Anostomus intermedius* sp. nov.
Snout length 43–44 per cent of head length; vertical pigmented areas present below lateral line9
9. Lateral line scales 40–42; caudal peduncle length about equal to its depth; vertical pigmented areas two scales wide (Nickerie, Surinam) *Anostomus spiloclistron*
Lateral line scales 38–39; caudal peduncle length less than its depth; vertical pigmented areas one scale wide (Essequibo, Guyana) *Anostomus plicatus*
10. Colour pattern in alcohol consisting of longitudinal lines of dark spots in centres of scales with no vertical pigmented areas across dorsal midline; angle between posterior three primary radii on scales below dorsal fin 40–90° (Orinoco, Negro and Mato Grosso) *Pseudanos gracilis*
Colour pattern in alcohol always of vertical pigmented areas across dorsum, and two to four large blotches or spots (covering more than one scale) centred on lateral line; angle between posterior three primary radii on scales below dorsal fin 110–180°11
11. Colour pattern in alcohol with dark spots in centres of scales (Orinoco, Guyana) *Pseudanos irinae* sp. nov.
Colour pattern in alcohol with centres of scales light (Amazon south of the Negro) *Pseudanos trimaculatus*

Clave Artificial para los Géneros y Especies de los Anostominae

- 1. Dientes simfíseos (medios) de la mandíbula inferior parcialmente iguales a los que los rodean (laterales); mandíbula inferior (hueso sin dientes) igual de largo que de ancho; labios sin papilas dérmicas (puede ser arrugado)4
Dientes simfíseos (medios) de la mandíbula inferior alargados; mandíbula inferior (hueso sin dientes) más larga que ancha; labios con papilas dérmicas muy claras2
- 2. Escamas circumpedunculares 16, altura de la cabeza 80 a 90 por ciento del largo de si misma; un solo diente en cada lado de la mandíbula inferior (bifurcación Orinoco/Casiquire) *Gnathodolus bidens*
Escamas circumpedunculares 12, altura de la cabeza menos del 80 por ciento del largo de si; tres a cuatro dientes en la mandíbula inferior3
- 3. Mandíbula inferior cinco veces más larga que ancha, inclinada posterodorsalmente cuando la boca está completamente cerrada; tres dientes en la mandíbula inferior; el par simfíseo es cinco veces más alto que ancho y se proyectan sobre la mandíbula superior cuando la boca está cerrada (Xingu superior) *Sartor respectus*
Mandíbula superior dos veces más larga que ancha, vertical cuando la boca está cerrada; cuatro dientes en la mandíbula inferior, dientes simfíseos (medios) dos veces más altos que anchos (sistema Orinoco y superior Xingu) *Synoptolaemus cingulatus*
- 4. Colorido con más de una banda longitudinal y cada banda más ancha que una escama (en un fondo pálido)5
Colorido en bandas longitudinales de no más de una escama de ancho; con dos a cuatro manchas oscuras, o bien manchas a lo largo de la línea lateral (excepto en algunos individuos ó en *P. gracilis* donde una sola banda centrada en la línea lateral puede estar presente, y no manchas ocurren)7
- 5. Tres radios branquiostegos; una banda clara a lo largo de la región predorsal media; una hilera de manchas claras en la parte anterior del lomo (tributarios del sudeste del Amazonas, sistema del Orinoco y afluentes del Sur hasta Surinam) *Anostomus ternetzi*
Cuatro radios branquiostegos (primer radio puede estar reducido); una banda longitudinal oscura a lo largo de la región predorsal; no manchas presentes6
- 6. Mayor altura del cuerpo 27.5–29.5 (\bar{x} = 27.9) por ciento SL; altura de la cabeza 78–85 (\bar{x} = 81.4) por ciento del largo de la cabeza; 12 vertebras caudales (incluyendo el centro ural y vertebras de la espina hemal que se encuentran un poco más adelante que el primer pterigioforo) (Guyana francesa) *Anostomus brevior*

- Mayor altura del cuerpo 16.0–28.5 (\bar{x} = 22.6) por ciento SL; altura de la cabeza 49.5–80 (\bar{x} = 66.2) por ciento del largo de la cabeza; generalmente 11 vertebras caudales (raramente 12–13) (sistema del Amazona y Orinoco y los afluentes del Orinoco a Surinam) *Anostomus anostomus*.
7. Cuatro radios branquiostegos; dientes simfíseos de la mandíbula inferior se hayan truncados en ejemplares de 60 mm SL o más; distancia del hocico al origen de la aleta pélvica, mayor que la distancia desde el origen de la aleta dorsal al origen de la aleta caudal8
Tres radios branquiostegos; dientes simfíseos bicúspidos (ocasionalmente truncados por el uso en especímenes >80 mm SL); distancia desde el hocico el origen de la aleta pélvica igual o menor que la distancia desde el origen de la aleta dorsal al origen de la aleta caudal10
8. Largo del hocico 40 por ciento del largo de la cabeza; zonas verticales pigmentadas ausentes bajo la línea lateral (Xingu superior) *Anostomus intermedius* sp. nov.
Largo del hocico 43–44 por ciento del largo de la cabeza; zonas verticales pigmentadas presentes bajo la línea lateral9
9. 40–42 escamas en la línea lateral; largo del pedúnculo caudal, casi igual a su altura zonas verticales pigmentadas dos escamas de ancho (Nickerie, Surinam) *Anostomus spiloclistron*
Escamas en la línea lateral 38–39; largo del pedúnculo caudal menos que su altura; zonas verticales pigmentadas de una escama de ancho (Essequibo, Guyana) *Anostomus plicatus*
10. Colorido en alcohol muestra bandas longitudinales con lunares oscuros en el centro de las escamas; sin areas verticales pigmentadas a través de la línea media dorsal; ángulo entre los tres radios primarios posteriores de las escamas bajo la aleta dorsal 40–90° (Orinoco, Negro y Matto Grosso)11
Colorido en alcohol siempre con areas verticales pigmentadas a través del lomo, y dos a cuatro manchas grandes o pequeñas (cubriendo más de una escama) centradas en la línea lateral; ángulo entre los tres radios primarios posteriores de las escamas bajo la aleta dorsal 110–180°11
11. Colorido en alcohol con manchas negras en el centro de las escamas (Orinoco, Guyana) *Pseudanos irinae* sp. nov.
Colorido en alcohol con centros de las escamas claros (Amazona, sur del Negro) *Pseudanos trimaculatus*

***Anostomus* (Gronow) Scopoli 1777**

Anostomus Gronow 1763:122 (description and figure, no species mentioned, work not accepted by ICZN).

Anostomus Scopoli 1777:451 (not seen, compiled from Myers 1950:191. No species mentioned, but based on Gronow and therefore type species, by monotypy, must be that illustrated by Gronow 1756 which is *Salmo anostomus* Linnaeus).

Anostoma Rafinesque 1815 (not seen, compiled from Myers 1950:191. Emendation of *Anostomus*).

Mormyrhynchus Swainson 1839:186, 291 (type by monotypy. *M. gronoveii* Swainson, based on Gronow 1763, pl. 7, fig. 2 which is reproduced from Gronow 1756, and is thus *Salmo anostomus* Linnaeus).

Histiodromus Gistel 1848 (not seen, compiled from Myers 1950:191. Type by monotypy *Salmo anostomus*).

Pithecocharax Fowler 1906:319 (type by original designation, *Salmo anostomus* Linnaeus).

Diagnosis

Anostomus may be distinguished from *Sartor* and *Synaptolaemus* by presence of 16 circumpeduncular scales (vs 12) and from *Gnathodolus* by possession of 4 lower jaw teeth (vs 1). Species of *Anostomus* may be further distinguished from these genera in having a bony lower jaw (without teeth) as long as wide (vs longer than wide) and by absence of conical or rounded dermal papillae on lower jaw (vs papillae present). Species of *Anostomus* may be distinguished from *Pseudanos* by presence of four branchiostegal rays (except *A. ternetzi*, which, like *Pseudanos*, has three), in usually having 40 or fewer lateral line scales and 38 or fewer vertebrae (vs 41 or more scales and 39 or more vertebrae). Numerous osteological differences are mentioned in the discussion section of this paper.

***Anostomus anostomus* (Linnaeus, 1758)**

Fig. 3

Salmo anostomus Linnaeus 1758:312 (original description based on Gronow 1756, type locality: "Indiis").

Anostomus Scopoli 1777 (no species mentioned, but based on *Salmo anostomus* Linnaeus).

Anostomus anostomus — Meuschen 1775:37 (not seen, compiled from Géry 1960); Myers 1950:192 (partim); Géry 1960 (subspecies); Myers and de Carvalho 1959 (feeding habits); Knöppel 1972 (diet).

Mormyrhynchus gronoveii — Swainson 1839:291.

Histiodromus anostomus — Gistel 1848.

Leporinus anostomus — Valenciennes, in Cuvier and Valenciennes 1849.

Anostomus salmoneus — Gronow 1854:153 (Ed. Gray).

Pithecocharax anostomus — Fowler 1906:319.

Diagnosis

A. anostomus may be distinguished from all other anostomines (except *A. brevior* and *A. ternetzi*) by its colour pattern of dark longitudinal stripes on a light background. It is differentiated from *A. brevior* in having a shorter caudal peduncle (4 per cent of the 212 specimens examined overlap with lower percentage limit of *A. brevior*) and a less deep body and head (1.4 per cent and 0.5 per cent overlap respectively; specimens which overlapped only did so in one of three characters mentioned). See Table 1. These differences are also apparent when using other morphometric parameters (Fig. 4, peduncle depth vs peduncle length; Fig. 5, body depth vs head length; Fig. 6, head depth vs head length). *A. ternetzi* also tends to have a longer caudal peduncle (\bar{x} 13.9 per cent SL — a single specimen with 10.1 per cent, all others above 13 per cent), and may be further separated in possessing three branchiostegal rays, a median light predorsal stripe and light spots on the dorsum (vs four branchiostegal rays, a dark median predorsal stripe and no light spots on the dorsum in *A. anostomus*).

Description

A fusiform, striped, compressed *Anostomus* (size range of specimens examined 36–107 mm SL), with a moderately elongated snout. The following measurements are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 83.8 (78.3–87.7), 0.016, 0.001; lower jaw to adipose-fin origin 88.3 (82.0–91.3), 0.013, 0.001; lower jaw to dorsal-fin origin 49.4 (46.3–52.1), 0.010, 0.001; lower jaw to pelvic-fin origin 52.2 (48.7–56.0), 0.013, 0.001; dorsal-fin origin to caudal-fin origin 52.8 (46.8–56.5), 0.013, 0.001; dorsal-fin origin to adipose-fin origin 40.0 (34.4–43.8), 0.013, 0.001; caudal peduncle length 11.6 (9.3–15.0), 0.010, 0.001; caudal peduncle depth 10.7 (9.0–12.7), 0.010, 0.001; head length 26.5, (23.4–31.9), 0.012, 0.001; body depth 22.6 (16.1–28.4), 0.026, 0.002; body width 12.3 (10.5–13.9), 0.006, 0.001.

As percentage of head length: preopercle length 73.8 (68.6–79.0), 0.017, 0.001; snout length 41.0 (36.1–46.1), 0.021, 0.001; head depth 66.2 (49.7–79.8), 0.070, 0.005; preopercle depth 54.0 (45.2–61.6), 0.033, 0.002; snout depth 34.2 (29.7–39.0), 0.016, 0.001; eye diameter 23.3 (18.9–28.0), 0.016, 0.001; bony interorbital 32.8 (29.6–36.3), 0.012, 0.001.

Lateral-line scales 39.3 (38–43, usually 39–40) 0.637, 0.044; dorsal transverse 4.5 (4–5), 0.151, 0.010; ventral transverse 3.8 (3.5–4.5), 0.306, 0.021; predorsal 11.7 (9–13), 0.807, 0.055; dorsal to adipose 12.9 (11–14), 0.626, 0.055; adipose to caudal 6.8 (6–8), 0.563, 0.049; isthmus to pelvis 17.2 (15–18), 0.735, 0.064; pelvis to anus 11.5 (10–13), 0.593, 0.050; anal to caudal 6.1 (5–8), 0.545, 0.048, circumpeduncular 16.

Scales (from scale row immediately above lateral line and in line with dorsal fin origin) divided roughly into quarters by four primary radii approximately at right angles (Fig. 7A) in specimens up to about 55 mm SL. Angle between the dorsal and ventral radii is thus about 180°. In larger specimens number of radii generally

increases (nine in a 107 mm SL specimen) and a few reticulations may appear around focus. Lateral-line scales usually with four posterior radii, one passing along the lateral-line tubule to posterior edge of scale (Fig. 7A).

Dorsal fin usually iii 10 (occasionally iv 9 or iii 9), caudal fin normally of 10 dorsal and 9 ventral principal rays (occasional variants with 9 or 11 upper, or 8 lower rays); anal usually iii 8 (rarely iii 7), pelvic i 8 (seldom i 7, and then usually on one side only); pectoral i 12 – i 16 (\bar{x} i 14.2, SD = 0.690, SE = 0.047). Number of olfactory lamellae increasing body size from 18 in 36.1–42.0 mm SL specimens to 38 in a specimen 90.6 mm SL; vertebrae usually 36 + ural centrum (with 11 caudal including ural centrum) range 35–39, \bar{x} = 36.2, SD = 0.787, SE = 0.186 (n=20). First pterygiophore of dorsal fin inserts between neural spines of eleventh and twelfth vertebrae. Four branchiostegal rays.

Teeth orange-brown, four in each half of both upper and lower jaws. Cusps fairly consistent, in upper jaw usually (from symphysis out posterolaterally) two cusps on first and second teeth, three on third and four on lateralmost tooth, in lower jaw, three cusps on first three teeth and lateralmost tooth with four cusps. Commonest variation found was wearing away of cusps of inner two upper jaw teeth and innermost lower jaw tooth, this virtually confined to a few individuals over about 85 mm SL. Upper jaw teeth point straight forward; those in lower jaw recurved, pointing posteriorly and somewhat dorsally, and lying outside upper jaw teeth when the mouth is fully closed.

Colour pattern in alcohol consists of a light background with black longitudinal stripes:

- 1) Median dorsal stripe begins between eyes and ends at last dorsal fin ray;
- 2) Dorsolateral stripe begins at base of upper jaw lips where it is more or less continuous with dorsolateral stripe of opposite side. Stripes join again on dorsal midline somewhat anterior to adipose fin, and continue posteriorly as a single stripe to caudal-fin rays. Stripe about one scale wide, and follows course of third scale row above lateral line;
- 3) Midlateral stripe begins at front of lower jaw and passes posteriorly through eye, across opercle, and along lateral-line scale row to base of caudal peduncle. It is usually somewhat irregular, and may extend half a scale row above and below lateral-line series;
- 4) Ventrolateral stripe begins on preopercle anterior to eye, crosses subopercle and base of pectoral fin, and continues posteriorly along third scale row below lateral line to meet stripe from opposite side at origin of anal fin. They then continue posteriorly as a single stripe to caudal-fin origin;
- 5) Midventral stripe begins at lower jaw and passes posteriorly across branchiostegal membrane to pelvic fins, and from there on to anus. In some specimens the region between isthmus and pelvic fins may possess a thin longitudinal light stripe in midline. Adipose fin black in very small specimens, becoming hyaline distally with a black spot at base in specimens about 60 mm SL, black pigment disappearing with increasing body size. Other fins hyaline.

In life, background is ivory-yellow, stripes being dark-brown to black. Dorsal, caudal, anal and sometimes pelvic fins are suffused with red, which is most intense on caudal and posterior rays of dorsal and anal fins. (Above description from aquarium specimens, locality unknown.)

Distribution

A. anostomus appears to have a wide distribution (Fig. 8), including the middle (Steindachner, 1882) and upper (Géry, 1960, and present study) Amazon, the Orinoco, and many of the rivers of Guyana and Surinam. Specimens from Guyana and Surinam are particularly abundant in museum collections, but this is an artifact of collecting effort. Géry (1960) recognized two subspecies, *A. anostomus anostomus* from the Orinoco/Guyana/Surinam region, and *A. a. longus* from the upper Amazon. Although the Rio Negro may well provide a geographic barrier (in terms of black water/white water preferences) between these populations, Géry distinguished them solely on the basis of body depth. My material from the Amazon (three paratypes of the subspecies) is insufficient to critically examine the reported difference, and I am somewhat sceptical of the usefulness of such a distinction. Be that as it may, there seems little doubt that the ranges of the two populations (based on available information) at one time overlapped, implying a more extensive distribution for this species in the past. Judging from the Surinam collections, *A. anostomus* seems to prefer sandy or muddy substrates in slowly flowing creeks of up to 1 m in depth. Knöppel (1972) reports that four specimens of the Amazonian population contained plant remains, algae, fungi, chitin remains, copepod crustacea and sand in their stomachs.

The species has also been recorded in the literature from Colombia (Florencia on the Orteguaza River which drains via the Caquetá and Japurá Rivers into the Amazon, (Fowler, 1943, 1945)), and from the Rio Jutai at its junction with the Amazon (Steindachner, 1882).

Variation

Several factors can effect the amount of variation found in fishes. Amongst these, two species of *Anostomus* have been shown to exhibit growth inflections (Winterbottom, 1974a). These occurred at approximately 75 mm SL, which may indicate the onset of sexual maturity. *A. anostomus* exhibits sexual dimorphism in the depth of the caudal peduncle. When plotted against standard length, the regression lines for males and that for females are well separated (Fig. 9). In a sample of 25 specimens (ZMA 106.528, Surinam) there were 10 males, 11 females and 4 immature. The immature specimens fall close to the line of regression for the females ($R^2 = 0.95$) and are quite well separated from that for the males (where $R^2 = 0.98$). This may indicate a linear growth in immature and female fish, but a growth inflection in the males. Onset of sexual maturity appears to occur between 60 and 65 mm SL (somewhat less than that postulated for *A. spiloclistron* and *A. plicatus* (75–80 mm SL) by Winterbottom (op. cit.)).

Anostomus brevior Géry, 1960

Fig. 10

Anostomus brevior Géry 1960:499 (original description, type locality: Camopi River, Oyapok river system, French Guiana); Knöppel, 1972 (gut contents).

Diagnosis

A. brevior is distinguishable from all other anostomines (except *A. ternetzi* and *A. anostomus*) by its colour pattern of dark longitudinal stripes on a light background. It may be distinguished from *A. anostomus* by its longer caudal peduncle and deeper body and head (Table 1; see also Figs. 4 to 6). In addition to the last two characters, it differs from *A. ternetzi* in having four branchiostegal rays (vs three) and a dark stripe along middle predorsum (vs a light stripe).

Description

A fusiform, somewhat deep bodied *Anostomus* (size range examined 69.1–86.5 mm SL) with a maximum recorded length of 91 mm SL (Géry, 1960). The following measurements are expressed as percentages, and these and the meristics consist of a mean with the range in parentheses.

As percentage of standard length: lower jaw to anal-fin origin 81.1 (79.2–83.3); lower jaw to adipose-fin origin 86.9 (86.3–88.2); lower jaw to dorsal-fin origin 50.0 (47.5–51.9); lower jaw to pelvic-fin origin 51.1 (49.7–52.4); dorsal-fin origin to caudal-fin origin 53.4 (51.8–54.4); dorsal-fin origin to adipose-fin origin 39.9 (37.4–42.4); caudal peduncle length 13.2 (12.6–14.1); caudal peduncle depth 11.1 (10.1–11.8); head length 25.5 (25.1–26.3); body depth 27.9 (27.4–29.5); body width 13.3 (12.7–13.8).

As percentage of head length: preopercle length 74.8 (74.6–75.3); snout length 39.8 (38.3–41.1); head depth 81.4 (78.8–84.8); preopercle depth 60.7 (58.1–63.6); snout depth 36.2 (33.3–38.1); eye diameter 21.4 (19.8–22.6); bony interorbital 34.5 (33.6–35.6).

Lateral-line scales 38.6 (38–39); dorsal transverse 5.0 (5); ventral transverse 4.0 (4); predorsal 11.6 (11–12); dorsal to adipose 13.0 (12–14); adipose to caudal 7.2 (7–8); isthmus to pelvis 16.8 (16–17); pelvis to anus 10.6 (10–11); anal to caudal 6.6 (6–7); circumpeduncular 16. Scale form as for *A. anostomus*.

Dorsal fin iii 10 (once iv 9), caudal fin of 10 dorsal and 9 ventral principal rays, anal iii 8, pelvic i 8, pectoral i 14 (once i 13). Number of olfactory lamellae increasing with body size, from 28 in a 73.2 mm SL specimen to 32 in a 81.5 mm SL specimen. Vertebrae usually 36 + ural centrum (once 37), with 12 (once 13) caudal vertebrae including ural centrum (\bar{x} = 36.2). First pterygiophore of dorsal fin inserts between neural spines of eleventh and twelfth vertebrae (once twelfth and thirteenth). Four branchiostegal rays. Teeth as for *A. anostomus*, as is colour pattern with a few minor differences. Dorsolateral stripes join at adipose fin origin (slightly more posteriorly than in *A. anostomus*), ventrolateral stripe is separated by a light stripe one scale row wide in ventral midline between isthmus and pelvis (as in some specimens of *A. anostomus*). Live colours as for *A. anostomus*, including red suffusion of fins (Géry, 1960).

Distribution

So far reported only from the Oyapok River system at its junction with the Camponi River and from the middle and upper Mana River at Cariacou and Dégrad Sanson respectively in French Guiana (Fig. 8). Knöppel (1972) reported the food of three specimens from the Mana River to consist primarily of detritus and diatomaceous algae.

Anostomus intermedius sp. nov.

Fig. 11

A. plicatus (non Eigenmann) — Géry, 1972–73 (upper Xingu, D'Arcy Thompson deformation coordinates); Knöppel, 1972 (upper Xingu, stomach contents — recorded as *A. plicatus* (?)).

Diagnosis

A. intermedius may be separated from the monotypic anostomine genera (*Gnathodolus*, *Sartor* and *Synaptolaemus*) by a combination of 16 circumpeduncular scales and four teeth in each half of the lower jaw. It may be separated from the striped *Anostomus* group (*A. anostomus*, *A. brevior* and *A. ternetzi*) by the possession of spots or blotches along the lateral line and dark bars across the dorsum. It may be differentiated from the species of *Pseudanos* by the truncate nature of symphyseal lower jaw teeth (vs bicuspid) in individuals larger than 60 mm SL, four branchiostegal rays (vs three), a greater snout to pelvic fin origin (\bar{x} = 57 per cent SL vs 51–52 per cent), shorter dorsal-fin origin to caudal-fin origin (51 per cent SL vs 54–55 per cent), a narrower interorbital (\bar{x} = 33 per cent HL vs 35–38 per cent), fewer lateral-line scales (\bar{x} = 39 vs 42–45) and vertebrae (\bar{x} = 36 vs 39–41). It differs from *A. spiloclistron* in the same way that *A. plicatus* does: a somewhat longer caudal peduncle (\bar{x} = 13 per cent SL vs 12 per cent), two less lateral line scales (\bar{x} = 39 vs 41), and two less vertebrae (\bar{x} = 36 vs 38). It differs from both these species in shorter snout length (\bar{x} = 40 per cent of head length vs 43–44 per cent; Figs. 12 and 13), in lacking any vertical pigmented areas below lateral line, and in fewer teeth on ceratobranchial 5 and fifth pharyngobranchial tooth plate.

Description

A. intermedius is a moderately elongate fusiform fish (size range of specimens examined 49–92 mm SL). The following measurements are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 81.5 (80.2–82.5), 0.007, 0.002; lower jaw to adipose-fin origin 86.3 (85.1–87.8), 0.008, 0.002; lower jaw to dorsal-fin origin 52.8 (50.3–54.6), 0.011, 0.003; lower jaw to pelvic-fin origin 56.7 (55.0–58.7), 0.008, 0.002; dorsal-fin origin to caudal-fin origin 50.7 (49.2–52.4), 0.009, 0.002; dorsal-fin origin to adipose-fin origin 35.6 (33.9–37.3), 0.009, 0.002; caudal peduncle length 13.1 (12.2–14.3), 0.006, 0.002; caudal peduncle depth 11.9 (11.6–12.3), 0.002, 0.001; head length 30.1 (27.8–31.9), 0.013, 0.003; body depth 27.2 (24.7–29.6), 0.012, 0.003; body width 14.3 (12.9–16.2), 0.009, 0.002.

As percentage of head length: preopercle length 72.7 (70.9–76.1), 0.013, 0.003; snout length 40.1 (38.9–42.1), 0.008, 0.002; head depth 74.8 (70.9–83.9), 0.040, 0.010; preopercle depth 60.8 (57.0–66.2), 0.025, 0.006; snout depth 36.0 (33.5–39.4), 0.020, 0.005; eye diameter 22.2 (20.5–24.0), 0.015, 0.004; bony interorbital 32.9 (30.4–35.0), 0.015, 0.004.

Lateral-line scales 38.9 (38–40), 0.515, 0.125; dorsal transverse 6, ventral transverse 4.5, predorsal 16.1 (15–17), 0.858, 0.208; dorsal to adipose 11.4 (10–13),

0.870, 0.211; adipose to caudal 6.8 (6–8), 0.636, 0.154; isthmus to pelvis 17.5 (17–21), 1.007, 0.244; pelvis to anus 9.4 (9–11), 0.618, 0.150; anal to caudal 6.3 (5–7), 0.686, 0.166; circumpeduncular 16. Scales from row above lateral line and from lateral line (below dorsal origin) as for *A. plicatus* (Fig. 7D).

Dorsal fin iii 10, caudal fin with 10 upper and 9 lower principal rays, anal fin iii 8, pelvic fins each i 8, pectoral fin i 14–i 16. Number of olfactory lamellae increasing with body size, from 22 in a 50 mm SL specimen to 36 in a 92 mm SL individual. Vertebrae 35.9 (35–37), plus ural centrum, with 11–12 caudal (including ural centrum) and first pterygiophore of dorsal fin inserting between neural spines of eleventh–twelfth or twelfth–thirteenth vertebrae. Four branchiostegal rays.

Teeth orange-brown, four in each half of each jaw. In upper jaw, symphyseal tooth tricuspid, next tooth tricuspid in individuals less than 55 mm SL, bicuspid in specimens larger than this, next tooth tricuspid (bicuspid in largest specimen), lateralmost tooth tricuspid. In lower jaw of specimens smaller than 55 mm SL, symphyseal and next tooth bicuspid, next and lateralmost teeth tricuspid. In larger specimens inner two teeth may be bicuspid, or, more usually, truncate.

Colour pattern of subadults in alcohol consisting of bars, about one scale row wide, over dorsum with spots and elongate blotches along the lateral line. The six to nine bars (which seldom reach the lateral line, and never extend significantly below it) are distributed as follows: four predorsal (last just anterior to dorsal origin), two across dorsal fin base, and three between the dorsal and adipose fins (these latter may be faint or absent). There are six to seven dark rounded blotches or elongated ovals along the lateral line, distributed as follows: first usually greatly elongate (sometimes separated into two blotches, the posterior one being small and rounded) covering lateral-line scales two to ten (if separated into two blotches, first on scales two to seven, second on nine to ten); third (or second) blotch larger and more intensely pigmented, lying on scales (including variation) 13–18; fourth blotch on scales 22–24; fifth blotch again darker, on scales 26–29; sixth blotch on scales 32–33, seventh blotch large, on scales 36–38. Third, fifth and seventh blotches cover lateral-line scales and extend half a scale row above and below, other blotches more or less confined to lateral line. In larger individuals there is a tendency for bars over dorsum to fade, while blotches along lateral line tend to elongate to form an intermittent lateral stripe. Posterior fields of scales light, surrounded by darker pigment. Both lips plicate.

Distribution

At present recorded only from the upper Xingu River, Amazon system (Fig. 14). Knöppel (1972) records the gut contents of this species (listed as *A. plicatus*? Eigenmann, 1912) as primarily filamentous algae, with plant remains, fungi, detritus, sand and chitin remains included in the diet.

Etymology

Named *intermedius* (to be treated as a noun in apposition) in allusion to its intermediate position in morphometric and colour pattern characteristics between *A. plicatus* and *A. spiloclistron* on the one hand and the genus *Pseudanos* on the other. (Note: this does not imply an intermediate phylogenetic position).

***Anostomus plicatus* Eigenmann, 1912**

Fig. 15

Anostomus plicatus Eigenmann 1912:296 (original description, type locality: Essequibo River, Guyana); Winterbottom 1974a (comparison with *A. spiloclistron*).

Diagnosis

A. plicatus may be separated from the monotypic anostomine genera by a combination of 16 circumpeduncular scales and 4 teeth in each lower jaw. It is distinguished from the striped *Anostomus* group (*A. anostomus*, *A. brevior* and *A. ternetzi*) by possession of two to four blotches along lateral line and dark narrow bars across dorsum. It is differentiated from *Pseudanos* and all remaining species of *Anostomus* (except *A. intermedius* and *A. spiloclistron*) by truncate nature of symphyseal lower jaw teeth (vs bicuspid), four branchiostegal rays (vs three), longer snout to pelvic-fin origin (\bar{x} = 56 per cent SL vs 51 per cent), shorter dorsal-fin origin to caudal fin (51 per cent SL vs 54–55 per cent SL), longer snout (\bar{x} = 44 per cent HL vs 38–39 per cent), narrower interorbital (\bar{x} = 33 per cent HL vs 35–38 per cent), fewer lateral-line scales (\bar{x} = 39 vs 42–45) and vertebrae (\bar{x} = 36 vs 39–41). Furthermore, at least some of narrow transverse bars across dorsum continue ventrally well below lateral line, sometimes to ventral midline (vs just reaching lateral line). It differs from *A. spiloclistron* in longer caudal peduncle (\bar{x} = 14 per cent SL vs 12 per cent — see Table 1) fewer lateral-line scales (\bar{x} = 39 vs 41) and vertebrae (\bar{x} = 36 vs 38) and in narrower transverse bars across dorsum (one scale wide vs two scales wide). It may be separated from *A. intermedius* by longer snout (\bar{x} = 44 per cent HL vs 40 per cent; Figs. 12 and 13), by possession of vertical pigmented areas below midline (vs absent below midline) and in having more teeth on ceratobranchial five and fifth pharyngobranchial tooth plate.

Description

A fusiform, somewhat compressed species of *Anostomus* (size range of specimens examined 58–111 mm SL) with a colour pattern of spots, bars and bands. The following measurements are expressed as percentages, and these and the meristic values consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 82.9 (81.1–85.2), 0.013, 0.004; lower jaw to adipose-fin origin 88.0 (86.0–89.5), 0.013, 0.004; lower jaw to dorsal-fin origin 52.8 (49.7–55.6), 0.017, 0.005; lower jaw to pelvic-fin origin 56.1 (53.4–60.1), 0.018, 0.005; dorsal-fin origin to caudal-fin origin 50.9 (48.2–53.0), 0.014, 0.004; dorsal-fin origin to adipose-fin origin 37.4 (35.3–40.8), 0.016, 0.005; caudal peduncle length 13.8 (12.5–15.7), 0.010, 0.003; head length 29.3 (27.2–32.2), 0.013, 0.004; body depth 27.1 (25.2–31.2), 0.018, 0.005; peduncle depth 11.8 (11.2–12.3), 0.004, 0.001; body width 12.3 (6.8–14.1), 0.019, 0.006.

As percentage head length: preopercle length 74.0 (71.8–76.1), 0.011, 0.004; snout length 43.9 (41.1–47.0), 0.014, 0.004; head depth 76.3 (70.6–82.1), 0.036, 0.010; preopercle depth 59.9 (56.6–64.0), 0.024, 0.007; snout depth 37.9

(34.4–41.2), 0.018, 0.005; eye diameter 23.4 (20.4–32.2) 0.031, 0.009; bony interorbital 32.8 (29.0–35.6), 0.020, 0.006.

Lateral-line scales 38.6 (38–39), 0.463, 0.129; dorsal transverse 4.9 (4.5–5.5), 0.463, 0.129; ventral transverse 4.4 (4.0–4.5), 0.219, 0.061; predorsal 11.8 (11–13); 0.832, 0.231; dorsal to adipose 11 (10–13), 0.913, 0.253; adipose to caudal 6.7 (5–9), 1.109, 0.308; isthmus to pelvis 16.2 (15–18), 0.832, 0.231; pelvis to anus 8.9 (7–10), 0.954, 0.265; anal to caudal 6.7 (5–8), 0.751, 0.208; circumpeduncular 16. Number of radii on scales (from below dorsal origin) increases with size, larger examples show reticulations starting at focus of the scale. Angle between posterior three primary radii about 90–180°. Lateral-line scales from below dorsal fin with a very variable number of radii, some show reticulations (Fig. 7D).

Dorsal fin iii 10; caudal fin normally of 10 upper and 9 lower rays (once 9 and 8 respectively); anal fin iii 8; pelvic fin i 8 (once i 7 on one side); pectoral fin i 12–i 16 (\bar{x} = i 15.3, SD 0.925, SE 0.257). Number of olfactory lamellae increasing with body size, from 32 in a 50 mm SL specimen to 48 in a specimen 110.9 mm SL. Vertebrae 35.6 plus ural centrum (35–36, SD = 0.480, SE = 0.147), with 11–12 caudal including ural centrum. First pterygiophore of dorsal fin lies between tips of eleventh and twelfth or, more commonly, twelfth and thirteenth, neural spines. Four branchiostegal rays.

Teeth four in each half of each jaw. Upper jaw teeth bicuspid in inner two (but prone to become worn down and truncated) and bi- to tricuspid in outer two. In lower jaw, inner two teeth are usually truncated, outer two are bi- or tricuspid.

Colour pattern in alcohol consists of dark spots, bars (vertical stripes not crossing midline) and bands (vertical strips across body) on a fawn background. Number of bars/bands variable, there being up to 14 in large specimens; all less than one scale wide. Four dark, somewhat elongated spots, one scale row wide on lateral line. Including variation, they may cover lateral-line scales 4 to 5, 14–18, 25–28 and 35–38. There is no record of live colouration, although there is some evidence that the centres of the scales are iridescent (Eigenmann, 1912; see Winterbottom, 1974a, for discussion).

Distribution

This species is at present only recorded from the Essequibo River System, Guyana, from Bartica near the mouth of the river to the savannah highlands drained by the Kuyuwini and Rupununi Rivers and the headwaters of the Essequibo (Fig. 14). Géry (1972–73) records *A. plicatus* from the upper Xingu River (a southern tributary of the Amazon) but these specimens are *A. intermedius*.

Variation

Winterbottom (1974a) has shown that certain characters exhibit a growth inflection, and suggested that this was due to the onset of sexual maturity. For example, a plot of preopercle depth versus preopercle length shows a marked inflection. That this is not a universal phenomenon in *Anostomus* is indicated by a comparison (of the same characters) with *A. anostomus*, where no inflection is apparent.

Anostomus spiloclistron Winterbottom, 1974

Fig. 16

Anostomus spiloclistron Winterbottom, 1974a:154 (original description, type locality: Nickerie River system, Surinam).

Diagnosis

A. spiloclistron is separated from the monotypic anostomine genera by combination of 16 circumpeduncular scales and four teeth in each lower jaw. It differs from the striped *Anostomus* group (*A. anostomus*, *A. brevior* and *A. ternetzi*) by possession of a two to four blotches along lateral line and dark narrow bars across dorsum. It may be distinguished from *Pseudanos* and all other species of *Anostomus* (except *A. intermedius* and *A. plicatus*) by truncate nature of symphyseal lower jaw teeth (vs bicuspid), four branchiostegal rays (vs three), longer snout to pelvic-fin origin (\bar{x} = 55 per cent SL vs 51 per cent), shorter dorsal-fin origin to caudal (\bar{x} = 51 per cent SL vs 54–55 per cent), longer snout (\bar{x} = 43 per cent HL vs 38–39 per cent), narrower interorbital (\bar{x} = 31 per cent HL vs 35–38 per cent), fewer lateral-line scales (\bar{x} = 41 vs 42–45) and vertebrae (\bar{x} = 38 vs 39–41) (Table 1). Further, at least some of narrow transverse bars across dorsum continue ventrally well below lateral line, sometimes to ventral midline (vs just reaching lateral line). It differs from *A. plicatus* and *A. intermedius* in a shorter caudal peduncle (\bar{x} = 12 per cent SL vs 14 per cent), more lateral-line scales (\bar{x} = 41 vs 39) and vertebrae (\bar{x} = 38 vs 36) and in wider transverse bars across dorsum (two scales wide vs one scale wide). It can be separated from *A. intermedius* by longer snout (\bar{x} = 43 per cent HL vs 40 per cent; Figs. 12 and 13), by presence of vertical pigmented areas below lateral line (vs absent) and in having more teeth on ceratobranchial five and fifth pharyngobranchial tooth plate.

Description

A moderately elongate fusiform species of *Anostomus* (size range of specimens examined 59–104 mm SL). The following measurements are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 83.9 (82.1–85.4), 0.010, 0.003; lower jaw to adipose-fin origin 88.9 (86.8–90.2), 0.010, 0.003; lower jaw to dorsal-fin origin 51.2 (49.8–52.7), 0.007, 0.002; lower jaw to pelvic-fin origin 55.1 (53.6–57.2), 0.009, 0.002; dorsal-fin origin to caudal-fin origin 51.3 (49.4–53.4), 0.013, 0.003; dorsal-fin origin to adipose-fin origin 38.7 (36.0–40.9), 0.014, 0.004; caudal peduncle length 11.5 (10.7–12.5), 0.005, 0.001; caudal peduncle depth 11.6 (10.7–12.3), 0.005, 0.001; head length 29.1 (26.6–30.9), 0.012, 0.003; body depth 25.8 (24.2–29.7), 0.005, 0.001; body width 13.6 (12.2–15.9), 0.010, 0.003.

As percentage of head length: preopercle length 73.8 (71.3–76.6), 0.015, 0.004; snout length 42.8 (41.6–45.1), 0.009, 0.002; head depth 69.1 (62.9–81.6), 0.058, 0.015; preopercle depth 54.0 (51.3–60.7), 0.028, 0.007, snout depth 33.9 (31.8–40.1), 0.024, 0.006; eye diameter 22.0 (19.6–23.5), 0.011, 0.003; bony interorbital 31.3 (30.1–33.9), 0.012, 0.003.

Lateral-line scales 41.0 (40–42), 0.423, 0.109; dorsal transverse 5.5; ventral transverse 4.5; predorsal 13.1 (12–14), 0.516, 0.133; dorsal to adipose 12.2 (11–14), 0.775, 0.200; adipose to caudal 7.0 (6–8), 0.378, 0.098; isthmus to pelvis 16.1 (15–17), 0.516, 0.133; pelvis to anus 11.2 (10–12), 0.561, 0.145; anal to caudal 6.6 (6–7), 0.507, 0.131; circumpeduncular 16. Scales from row above lateral line and in line with origin of dorsal fin with four radii in small specimens, increasing irregularly in number with increasing size, reticulations appear at the focus in larger specimens. Lateral-line scales as for *A. plicatus*.

Dorsal fin iii 10 or iv 9 (twice iii 9), caudal fin with ten upper and nine lower principal rays (once 10/10); anal fin iii 8, pelvic fins each i 8, pectoral fin i 15.0 (i 13–i 16), 0.945, 0.244. Number of olfactory lamellae increasing with body size, from about 30 at 60 mm SL to about 42 in specimens longer than 100 mm SL. Vertebrae 37.6 (37–38), 0.507, 0.131, plus ural centrum, with 12–13 caudal including ural centrum (once 11). First pterygiophore of dorsal fin inserting between neural spine tips of twelfth and thirteenth vertebrae (once eleventh and twelfth; holotype). Four branchiostegal rays.

Teeth orange-brown, four in each half of each jaw. In upper jaw inner three bicuspid (although in specimens less than about 65 mm SL middle two teeth may be tricuspid), outermost (most lateral), tooth is tricuspid. In lower jaw, inner two teeth truncate, outer two being tricuspid. In specimens below about 60 mm SL, outer of two truncate teeth may be bi- or even tri-cuspid.

Colour pattern in alcohol consists of dark spots, bars and bands on a light background. There are four round spots centred on lateral line, covering scale rows above and below lateral line; including variation the spots cover lateral-line scales 3 to 5, 13–18, 26–30 and 36–40. Bars and bands more variable. Bars normally present above lateral-line scales 1, 3, 14, 18, 28, and sometimes 36. Bands cross lateral line at scales 9, 22 and 33. Vertical pigmented areas that may form either bars or bands lie at lateral-line scales 6, 11 and 25. Bars usually have a ventral counterpart. Some individuals have light centres to scales.

Distribution

At present recorded only from the Fallawatra River of the Nickerie River system of western Surinam, close to the Stondansie Falls, in wide stretches of river (60–80 m) over sand and rock substrates (Fig. 14).

Variation

Certain characters show growth inflections apparently associated with the onset of sexual maturity (as in *A. plicatus*).

Anostomus ternetzi Fernandez-Yepe, 1949

Fig. 17

Anostomus ternetzi Fernandez-Yepe 1949:293 (original description, type locality: Orinoco River system); Géry 1960 (French Guiana); 1972/73 (upper Xingu River, D'Arcy Thomson deformation coordinates); Knöppel 1972 (diet).

Anostomus anostomus (non Linnaeus) — Myers 1950 (partim); Lowe 1964 (upper Essequibo River system).

Diagnosis

A. ternetzi differs from all other anostomines (except *A. anostomus* and *A. brevior*) in having dark lateral stripes on a light background. It can be separated from *A. anostomus* by its (usually) longer caudal peduncle (Fig. 4), its three branchiostegal rays (vs four) and by a light median predorsal stripe (vs dark median predorsal stripe). In addition to last two characters, which also separate it from *A. brevior*, it differs from that species in having a less deep body and head (Figs. 5 and 6).

Description

An elongate, striped species of *Anostomus* (size range of material examined 37–100 mm SL). The following measurements are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 81.2 (77.6–83.5), 0.013, 0.002; lower jaw to adipose-fin origin 87.4 (84.4–89.0), 0.011, 0.002; lower jaw to dorsal-fin origin 49.2 (47.4–51.6), 0.009, 0.002; lower jaw to pelvic-fin origin 51.9 (48.4–54.2), 0.011, 0.002; dorsal-fin origin to caudal-fin origin 52.8 (50.9–55.4), 0.010, 0.002; dorsal-fin origin to adipose-fin origin 39.4 (37.1–41.1), 0.010, 0.002; caudal peduncle length 13.9 (10.1–16.0), 0.011, 0.002; caudal peduncle depth 10.2 (9.2–11.4), 0.006, 0.001; head length 26.0 (24.3–29.9), 0.011, 0.002; body depth 20.9 (18.8–22.9), 0.012, 0.002; body width 11.6 (10.0–13.2), 0.008, 0.002.

As percentage head length: preopercle length 73.5 (70.1–75.8), 0.014, 0.002; snout length 40.3 (34.4–43.6), 0.022, 0.004; head depth 61.5 (53.6–68.6), 0.034, 0.006; preopercle depth 50.8 (45.9–53.7), 0.018, 0.003; snout depth 32.8 (30.2–36.3), 0.014, 0.002; eye diameter 22.6 (19.8–25.6), 0.015, 0.002; bony interorbital 31.6 (28.9–34.3), 0.011, 0.002.

Lateral-line scales 40.2 (39–42), 0.516, 0.084; dorsal transverse 4.6 (4.5–5), 0.223, 0.036; ventral transverse 3.8 (3.5–4), 0.250, 0.041; predorsal 12.3 (11–14), 0.694, 0.113; dorsal to adipose 13.0 (12–15), 0.676, 0.135; adipose to caudal 7.4 (6–9), 0.700, 0.140; isthmus to pelvis 16.8 (15–18), 0.851, 0.170; pelvis to anus 10.3 (9–11), 0.503, 0.082; anal to caudal 7.3 (6–8), 0.542, 0.108; circumpeduncular 16. Scales (from below dorsal origin) with four radii at right angles to each other in small (and sometimes large) individuals, with a tendency to increase number of radii with size. Reticulations often present in larger specimens (>62 mm SL). Lateral-line scales with a variable number of radii and sometimes a few reticulations.

Dorsal fin usually iii 10 (iv 9 three times, iii 9 once), caudal fin usually with 10 upper and 9 lower principal rays (once 9/9); anal iii 8 (once iii 7); pelvic i 8; pectoral i 13.7 (11–15), 0.653, 0.106. Number of olfactory lamellae increasing with specimen size, from 18 at 36.8 mm SL to 38 at 71.0 mm SL. Vertebrae usually 37 + ural centrum (with 12–13 caudal including ural centrum), range 37–38, $\bar{x} = 37.3$ ($n = 21$). Pterygiophore of first dorsal fin ray lies between neural spine tips of eleventh and twelfth or more commonly twelfth and thirteenth vertebrae. Three branchiostegal rays.

Teeth orange-brown, four in each half of each jaw. In upper jaw innermost two teeth on each side bicuspid, third tooth tricuspid, and outermost (most lateral) may have three or four cusps. Same applies to outermost tooth in lower jaw, other three teeth tricuspid. In one specimen (MZUSP 9989, 74.0 mm SL) all teeth in both jaws were truncate.

Colour pattern in alcohol consists of a series of dark longitudinal stripes on a light background. A thin light band passes from between nostrils to dorsal fin origin in middorsal line. This band flanked by a series of four poorly defined dark stripes, which are separated only by light spots in centre of each scale, thus forming a string of spots down each scale row. These become diffuse below dorsal fin, and region posterior to the dorsal fin is dark. A light stripe about one scale wide and centred between two scale rows above the lateral line, passes from top of eye to base of caudal fin. Ventral to light stripe, midlateral dark stripe begins at anterior margin of lower jaw, passes posteriorly through eye, across opercle and along lateral line to caudal base; it covers lateral-line scale row and half scale of rows above and below lateral line. Ventrolateral dark stripe begins on preopercle below eye, crosses subopercle and pectoral fin base, joins stripe from other side at anal fin, and continues posteriorly to base of caudal fin as a single median stripe; it is about one scale wide, centred on third scale row below lateral line. Midventral stripe starts at isthmus and passes posteriorly to anus. From pectoral fin area to origin of pelvic fins, it is separated into two lateral halves by a narrow, median white strip. Base of the adipose fin in all specimens is black, and marginal scales of caudal fin dark.

Distribution

A. ternetzi appears to be more or less confined to the eastern half of South America (Fig. 8). I have examined specimens from the Orinoco River system, from the upper Essequibo system, the headwaters of the Rio Branco (which drains into the Amazon via the Rio Negro), from the Tapajós River which flows northwards to the Amazon, from the upper Xingu River and from the mouth of the Tocantins River (which reaches the sea just south of the mouth of the Amazon). Géry (1960) reports specimens from the upper Maroni basin of French Guiana, as well as from the Araguaia, a tributary of the Tocantins (Géry, 1972/73).

Variation

Sex was determined in a single sample of 12 specimens (MZUSP 9990). Results indicate that the depth of the caudal peduncle is less in females than in males, but the difference does not appear to be as clear cut as it is in *A. anostomus*.

Genus *Gnathodolus* Myers 1927

Gnathodolus Myers 1927:108 (type by original designation *G. bidens* Myers).

Diagnosis

The genus may be distinguished from all other anostomines by its deep body (head

depth 80–90 per cent head length) and by the presence of a single cusped tooth in the lower jaw (vs 3–4 lower jaw teeth). In addition, it has a deeper caudal peduncle (\bar{x} = 13 per cent SL vs 9–12 per cent), a longer snout to preopercle length (\bar{x} = 81 per cent HL vs 70–75 per cent), a greater head depth (\bar{x} = 88 per cent HL vs 62–81 per cent), snout depth (\bar{x} = 51 per cent HL vs 33–45 per cent) and interorbital width (\bar{x} = 40 per cent HL vs 32–38 per cent). It differs from other two monotypic genera (*Synaptolaemus* and *Sartor*) in possessing 16 circumpeduncular scales. It shares with these genera (but differs from *Pseudanos* and *Anostomus*) a longer caudal peduncle (\bar{x} = 16–17 per cent SL vs 12–14 per cent), fewer vertebrae (\bar{x} = 35 vs 36–41) and presence of rounded or conical dermal papillae on lower jaw (Fig 19). It shares with *Sartor* (but not *Synaptolaemus*, *Pseudanos* or *Anostomus*) a wider body (\bar{x} = 16 per cent SL for *Sartor*, 19 per cent for *Gnathodolus* vs 11–14 per cent) deeper preopercle depth (70 per cent HL for *Sartor*, 75 per cent for *Gnathodolus* vs 51–64 per cent) and greater eye diameter (\bar{x} = 26 per cent HL for both vs 21–24 per cent). *Gnathodolus* differs from *Sartor* in wider body and deeper preopercle depth. (See above.)

***Gnathodolus bidens* Myers, 1927**

Fig. 18

Gnathodolus bidens Myers 1927:108 (original description, type locality: Casiquiare River in region of bifurcation with Orinoco).

Diagnosis

As for genus.

Description

A deep-bodied form with a size range of material examined 73 to 109 mm SL. As only three specimens were available for study, data will be presented as a mean followed by the range in parentheses.

As percentage standard length: lower jaw to anal-fin origin 79.1 (76.0–81.9), lower jaw to adipose-fin origin 84.9 (84.0–85.7), lower jaw to dorsal-fin origin 49.4 (49.0–49.7); lower jaw to pelvic-fin origin 51.8 (49.0–53.3); dorsal-fin origin to caudal base 55.0 (53.5–57.0); dorsal-fin origin to adipose-fin origin 38.3 (37.6–39.0); peduncle length 16.0 (15.3–16.6); peduncle depth 13.3 (13.1–13.7); head length 30.6 (30.0–31.3); body depth 30.0 (29.0–30.7); body width 19.3 (14.8–26.2).

As percentage of head length: preopercle length 81.4 (77.3–87.0); snout length 44.6 (43.0–45.8); head depth 87.6 (85.8–90.0); preopercle depth 74.5 (70.0–78.2); snout depth 51.0 (45.8–54.1); eye diameter 25.9 (25.6–26.2); bony interorbital 40.3 (38.8–42.0).

Lateral-line scales 39; dorsal transverse 5.5; ventral transverse 4.5; predorsal 11.0 (10–12); dorsal to adipose 11.0 (10–12); adipose to caudal 9.3 (9–10); isthmus to pelvis 16.0 (14–18); pelvis to anus 8.7 (8–9); anal to caudal 9; circumpeduncular 16. Scales (from below dorsal origin and one row above lateral line) with a variable number of radii increasing with size, reticulations at focus in larger individuals.

Lateral-line scales similar to *P. irinae*, with no radii along lateral-line tubule and no reticulations.

Dorsal fin iii 10, caudal with 10 upper and 9 lower principal rays, anal iii 8, pelvic i 8 (once i 7, one side only); pectoral i 15 (i 14–i 16). Vertebrae 35 + urostyle, with 13 caudal (including urostyle) and first pterygiophore of dorsal fin inserting between neural spines of tenth and eleventh vertebrae.

Four teeth in each upper jaw and one in lower. The upper jaw teeth have bluntly lanceolate points with a hint of lateral cusps. Lower jaw tooth is greatly elongated, with a sickle-shaped tip. It is somewhat recurved, with a concave posterior face. This pair of teeth projects above upper jaw when mouth is closed.

Colour pattern dull brown with six to eight diffuse darker crossbars dorsal to but not reaching lateral line. A diffuse black spot centred on lateral line below dorsal fin and a smaller one dorsal to anal fin. In life, scales with indistinct, light centres, suborbital area tinged with violet (Myers, 1927).

Distribution

Known only from the region of the Casiquiare/Orinoco bifurcation in Venezuela (Fig. 8).

Discussion

Myers (1950) reported that the paratype at the California Academy of Sciences (CAS) had been mislaid. As can be seen from the list of material, it has subsequently been located. The figure of the holotype (by Pablo Bravo) shows 10 ventral caudal rays, 7 branched pelvic fin rays and 32 lateral line scales (all incorrect). A radiograph of the holotype does reveal the presence of an abnormal extra caudal fin ray, the base lying above the lateral line but well removed from the distal end of hypural three. The peculiar structure of the caudal fin commented on by Myers (1927, 1950) seems to me to be due to injury (in spite of it occurring in two of the three types, the third specimen with a damaged caudal), the fin rays showing very definite signs of regeneration and previous injury. Radiographs also reveal the presence of a minute nubbin of bone at the anterior of the anal fin, which may represent an unbranched fin ray (giving a formula for the anal fin of iv 8).

Gnathodolus sp.

Fig. 19

Description

A single specimen referable to *Gnathodolus* was obtained by Mr. G. Howes of the British Museum (Natural History). It may well represent a new species, but is not so described since it is smaller than any of the types, there is only one specimen, and it comes from the aquarium trade. (The dealer thought it was probably collected in Columbia, Orinoco River system, Vichada River (G. Howes, pers.comm.).) It differs from *G. bidens* in having fewer lateral-line scales (36/37) and in colour pattern. Compared to *G. bidens* it has greater values for lower jaw to anal-fin origin (76.9 per cent SL) and eye diameter (27.6 per cent HL), and lesser values for lower jaw to

dorsal fin origin (47.8 per cent SL); body depth (27.4 per cent SL); peduncle depth (12 per cent SL); body width (14.8 per cent SL); snout length (39.3 per cent HL); head depth (75.5 per cent HL); preopercle depth (66.3 per cent HL) and bony interorbital (35.6 per cent HL).

Colour pattern in alcohol light yellow with about nine diffuse transverse bars across dorsum which do not reach lateral line. First three (predorsal) bands narrow and distinct, next two (bisected by dorsal fin) have a fair amount of pigment in interspace between them and could be interpreted as a single broad bar with darker edges. Three narrow bars present between dorsal and adipose fins and some indication of another bar between adipose and caudal fins. Two dark spots on lateral line, one, larger, beneath posterior base of dorsal fin and other below adipose fin origin. In addition a dark spot in second scale row below fourth lateral line scale.

Dentary tooth has a bicuspid tip, with a posterior projection or cusp on shaft of tooth (Fig. 19). Upper lip is plicate, while lower lip has conical papillae also found in *Synaptolaemus* and *Sartor*. Mr. Howes informs me that he observed this specimen in an aquarium removing scales from the flanks of a large *Schizodon* sp.; it also took commercial flake fish food.

Genus *Pseudanos* gen. nov.

Schizodon trimaculatus Kner 1859:161 (type species).

Diagnosis

Pseudanos differs from the monotypic anostomines (*Gnathodolus*, *Sartor*, *Synaptolaemus*) by a combination of 16 circumpeduncular scales and 4 teeth in each half of lower jaw. Bony portion of lower jaw is as long as it is wide, and lower lip is plicate (without conical or rounded dermal papillae). It may be differentiated from *Anostomus* by presence of three branchiostegal rays (except for *A. ternetzi*, species of *Anostomus* have four), and in having 41 or more lateral-line scales and 39 or more vertebrae (vs 40 or fewer lateral-line scales and 38 or fewer vertebrae). The numerous osteological differences between these two genera are described in the Discussion section of this paper.

Etymology

Derived from *pseudo* (false) and the first four letters of the generic name *Anostomus*, in allusion to the very similar external appearance of the two genera. Gender: masculine.

Pseudanos gracilis Kner, 1859

Fig. 20

Schizodon gracilis Kner 1858:160 (original description, type locality: Rio Guapore, Brazil).

Anostomus gracilis — Myers 1950 (new record from Orinoco drainage); Knöppel 1972 (diet).

Diagnosis

P. gracilis may be distinguished from the monotypic *Gnathodolus*, *Sartor* and *Synaptolaemus* by a combination of 16 circumpeduncular scales and a lower jaw with four teeth. It is distinguished from striped *Anostomus* group in that it has two to four round blotches or a single dark horizontal stripe along lateral line (never more than one stripe). It can be separated from spot-barred species (*P. irinae*, *P. trimaculatus*, *A. plicatus*, *A. intermedius* and *A. spiloclistron*) in that it never has narrow transverse bars across dorsum. It has a generally more slender and narrower body (body depth \bar{x} = 23 per cent SL vs 26–27 per cent; body width \bar{x} = 11 per cent SL vs 12–14 per cent; Table 1), and it has an angle between posterior three radii of scales (from row below dorsal fin origin and just above lateral line) of 40–90° (vs 110–180° — compare Fig. 7, A and C with B). *P. gracilis* may be further differentiated from *A. plicatus* and *A. spiloclistron* in having origin of pelvic fins nearer snout (\bar{x} = 51 per cent SL vs 55–56 per cent), a greater dorsal-fin origin to caudal-fin distance (\bar{x} = 54 per cent SL vs 51 per cent), a shorter snout (\bar{x} = 39 per cent HL vs 43–44 per cent), wider interorbital (\bar{x} = 35 percent HL vs 31–33 per cent), more lateral-line scales (\bar{x} = 45 vs 39–41) and vertebrae (\bar{x} = 41 vs 37–38) — see Table 1 — and three branchiostegal rays (vs four).

Description

A compressed fusiform species of *Pseudanos*, size range of material examined 41–161 mm SL. The following morphometrics are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation, and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 81.0 (79.6–83.9), 0.010, 0.002; lower jaw to adipose-fin origin 86.6 (85.1–88.8), 0.008, 0.002; lower jaw to dorsal-fin origin 48.6 (46.3–53.0), 0.016, 0.005; lower jaw to pelvic-fin origin 50.9 (48.4–54.9), 0.018, 0.004; dorsal-fin origin to caudal-fin origin 54.4 (49.9–57.4), 0.019, 0.004; dorsal-fin origin to adipose-fin origin 39.6 (35.9–42.6), 0.015, 0.003; peduncle length 12.7 (11.0–14.1), 0.008, 0.002; peduncle depth 9.4 (8.4–10.2), 0.005, 0.001; head length 26.3 (23.5–30.1), 0.021, 0.004; body depth 22.9 (18.3–25.4), 0.020, 0.004; body width 11.2 (10.4–11.9), 0.011, 0.008.

As percentage of head length: preopercle length 71.8 (68.4–76.4), 0.017, 0.003; snout length 38.5 (35.0–42.6), 0.021, 0.004; head depth 73.5 (57.5–85.8), 0.079, 0.016; preopercle depth 59.7 (51.1–67.5), 0.043, 0.008; snout depth 38.0 (29.8–45.8), 0.037, 0.007; eye diameter 24.1 (19.7–31.3), 0.024, 0.005; bony interorbital 35.0 (29.8–40.2), 0.024, 0.005.

Lateral-line scales 44.8 (43–47, the latter value from a specimen with a distorted lateral line on one side), 0.791, 0.115; dorsal transverse 5.0 (4.5–5.5), 0.141, 0.028; ventral transverse 4.0 (4–4.5), 0.098, 0.019; predorsal 13.4 (11–15), 0.852, 0.167; dorsal to adipose 14.5 (14–15), 0.707, 0.500; adipose to caudal 7.5 (7–8), 0.707, 0.500; isthmus to pelvis 17.5 (17–18), 0.707, 0.500; pelvis to anus 12.9 (11–14), 0.816, 0.160; anal to caudal 7.0 (6–8), 1.414, 1.000; circumpeduncular 16. Scales (from below dorsal origin) usually with three primary radii close together (between 40–90° apart, see Fig. 7B) on posterior field, one to middle of anterior field (45.7–136.4 mm SL). However, occasional specimens have scales with more

numerous radii and a few reticulations around focus (86.2 and 160.5 mm SL). Lateral-line scales with three radii, otherwise similar to *A. anostomus* (Fig. 7A).

Dorsal fin iii 10, caudal fin with ten upper (once nine) and nine lower principal rays, anal iii 8, pelvic i 8, pectoral i 13–i 16 (\bar{x} = i 13.9), 0.657, 0.129. Olfactory lamellae increasing in number with body size, 22 (41.1 mm SL) to 56 (152.5 mm SL). Vertebrae usually 41 + ural centrum, (with 13 caudal including ural centrum), range 40–42, SD = 0.535, SE = 0.189. First pterygiophore of dorsal fin lies between neural spines of twelfth and thirteenth or thirteenth and fourteenth vertebrae. Three branchiostegal rays.

Four teeth in each half of each jaw. In upper jaw, all tricuspid (medial two teeth sometimes bicuspid). In lower jaw medial two teeth bicuspid, next tooth tricuspid, lateralmost tooth with four cusps. The cusps tend to wear down very rapidly, for in a 91.3 mm SL specimen cusps are not evident and teeth are truncate.

Colour pattern in alcohol variable. There are usually 11 thin stripes on body, these produced by elongated dark spots in centre of each scale on a tan background. Stripes thus pass along centre of each scale row. Median predorsal stripe present. Many specimens exhibit dark spots on the flanks between lateral-line scale row and row ventral to it. Number of spots is somewhat variable (first is sometimes absent, and third indistinct). Including individual variation, first spot covers lateral-line scales 4 to 6, second 16–18, third 30–32 and fourth 41–45. In other individuals, spots may be replaced by a dark stripe which extends from shoulder girdle to caudal peduncle between lateral line and scale row below. No specimens with both a dark stripe and spots have been seen; in any collection, all specimens have either one or the other colour pattern only. Specimens from the bifurcation of the Orinoco at Laja Tama Tama and a single specimen from the Orinoco at Caicara have the dark stripe and no spots. However, specimens from a locality on the Orinoco between the above collection sites (at San Fernando where the Atabapo joins the Orinoco) have no dark stripes, but do possess the four dark spots. I can find no differences whatsoever in the morphometric or meristic data to justify separation at any taxonomic level. Whether the colour difference is ecophenotypic, genetic or due to some other factor(s) must await extensive collecting and monitoring of environmental conditions. Colour in life is partly opposite that in alcohol. In two Kodachromes of aquarium specimens (one by S. H. Weitzman & W. L. Fink, USNM uncat., the other by K. Paysan, courtesy of TFH Publications) the centres of the scales are an almost iridescent yellow. In the USNM specimen, the lateral line is dark grey, as is the rest of the fish, the dorsal and caudal fins being tinged with red. On preservation, this specimen exhibited the dark lateral stripe with elongated dark spots in the centres of the scales on a light tan background. In Paysan's specimen, on the other hand, the background colour is a fairly light greenish-brown, four dark spots are present along the lateral line, and the lateral line scales between these spots have light centres. The dorsal and caudal fins and the mouth are red. I have not seen this specimen preserved.

Distribution

The vast majority of specimens in museum collections come from the Orinoco River system (Fig. 14). The species is, however, known from a number of localities in the Amazon system (San Carlos de Rio Negro, on the Negro River near the mouth of the Casiquaire Canal, from Manaus on the Negro, and from the type locality the Guaporé River, which drains into the Amazon via the Madeira River). Knöppel (1972)

reported on the diet of specimens from Igapou Castanha (mid-region of the Negro) which consisted mainly of plant remains, as well as fungi, algae, detritus, sand, chiton remains and terrestrial insects.

***Pseudanos irinae* sp. nov.**

Fig. 21

Anostomus trimaculatus (non Kner, 1859) Eigenmann 1912 (Essequibo River); Myers 1950 (upper Orinoco); Ramirez 1957 (Venezuela); Mago-Leccia 1970 (Venezuela).

Diagnosis

P. irinae may be distinguished from *Gnathodolus*, *Sartor* and *Synaptolaemus* by a combination of 16 circumpeduncular scales and four lower jaw teeth. It may be distinguished from the striped *Anostomus* group (*A. anostomus*, *A. brevior* and *A. ternetzi*) by the presence of two to four rounded blotches along the lateral line, and narrow transverse bars across the dorsum. It can be separated from *A. plicatus*, *A. intermedius* and *A. spiloclistron* by cusped nature of symphyseal lower jaw teeth (vs truncate), pelvic origin closer to snout ($\bar{x} = 51$ per cent SL vs 55–56 per cent), dorsal-fin origin to caudal fin distance greater ($\bar{x} = 55$ per cent SL vs 51 per cent), a shorter snout length ($\bar{x} = 39$ per cent HL vs 43–44 per cent), a wider interorbital ($\bar{x} = 38$ per cent HL vs 31–33 per cent), more lateral-line scales ($\bar{x} = 43$ vs 39–41) and vertebrae ($\bar{x} = 40$ vs 36–38) and three (vs four) branchiostegal rays. It differs from *P. gracilis* in having a deeper ($\bar{x} = 26$ per cent SL vs 23 per cent) and wider ($\bar{x} = 13$ per cent SL vs 11 per cent) body, generally having two less lateral-line scales ($\bar{x} = 43$) and one less vertebra ($\bar{x} = 40$) (Table 1), presence of narrow dark transverse bands across dorsum, and an angle of 110–180° between three posterior scale radii (vs 40–90°). It can be separated from *P. trimaculatus* in its usually narrower body ($\bar{x} = 13$ per cent SL vs 14 per cent, Fig. 22), average of one more lateral-line scale (43) and vertebra (40), and by a dark spot in centre of each scale (vs a light spot).

Description

A fusiform, somewhat compressed species of *Pseudanos* with a colour pattern of spots and bars, and a size range of material examined of 54–100 mm SL. The following measurements are expressed as percentages, and these and the meristic values consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 81.3 (78.7–83.7), 0.011, 0.002; lower jaw to adipose-fin origin 86.8 (84.6–89.3), 0.009, 0.001; lower jaw to dorsal-fin origin 49.3 (46.9–51.1), 0.011, 0.001; lower jaw to pelvic-fin origin 51.3 (48.4–53.9), 0.012, 0.002; dorsal-fin origin to caudal-fin origin 55.0 (52.9–57.7), 0.010, 0.001; dorsal-fin origin to adipose-fin to origin 40.3 (37.4–43.4), 0.012, 0.002; caudal peduncle length 13.1 (11.8–14.7), 0.006, 0.001; peduncle depth 10.4 (9.4–11.8), 0.005, 0.001; head length 27.2 (24.8–29.1), 0.008,

0.001; body depth 26.4 (23.7–28.9), 0.010, 0.001; body width 13.0 (11.9–14.7), 0.006, 0.001.

As percentage of head length: preopercle length 70.3 (65.6–75.5), 0.020, 0.003; snout length 38.0 (34.0–41.9), 0.016, 0.002; head depth 81.5 (73.4–92.5), 0.039, 0.005; preopercle depth 63.7 (57.6–69.0), 0.027, 0.004; snout depth 37.9 (33.8–42.6), 0.017, 0.002; eye diameter 24.4 (20.3–28.7), 0.019, 0.003 (Fig. 23); bony interorbital 37.5 (34.5–41.2), 0.014, 0.002.

Lateral-line scales 43.2 (41–45), 1.047, 0.136; dorsal transverse 5.5, ventral transverse 4.5 (4.5–5.0), 0.091, 0.012; predorsal 13.2 (11–15), 0.760, 0.010; dorsal to adipose 13.2 (11–14), 0.690, 0.092; adipose to caudal 8.5 (7–10), 0.572, 0.077; isthmus to pelvis 17.1 (14–20), 1.257, 0.168; pelvis to anus 11.6 (10–13), 0.689, 0.090; anal to caudal 7.7 (6–9), 0.570, 0.076; circumpeduncular 16. Scales (from below dorsal origin) with four primary radii (three in posterior field), occasionally developing a few reticulations around focus in larger individuals. Lateral-line scales with 2–4 radii (Fig. 7C) none of which follow along lateral-line tube (as in *A. anostomus*).

Dorsal fin iii 10 (iv 10 and iv 9 twice each), caudal fin of 10 dorsal and 9 ventral principal rays (once with nine dorsal rays), anal fin iii 8 (twice iii 7), pelvic fins i 8 (twice i 7), pectoral fin i 13–i 16 (\bar{x} = 14.2). Olfactory lamellae increasing with body size, from 22 in a 53 mm SL specimen to 36 in an individual of 100.3 mm SL. Vertebrae 39–41 + ural centrum (\bar{x} = 40.0, SD = 0.894, SE 0.70) with 12–14 (\bar{x} = 12.8) caudal including ural centrum. First pterygiophore of dorsal fin inserts between neural spines of twelfth and thirteenth vertebrae. Three branchiostegal rays.

Teeth orange-brown, four in each half of each jaw. Considerable range in number of cusps that may be present. In upper jaw, innermost two teeth may have one to three (usually three) cusps, third tooth with two to four (usually three) cusps, outer (lateralmost) tooth with three to five cusps. In lower jaw, innermost two teeth with two to three (usually two) cusps, third tooth with three to four (usually three) cusps, and outer (lateralmost) tooth with four to five cusps.

Colour in alcohol yellow brown, paler below, with two to four dark spots or blotches along lateral line, covering scales three to five (this spot lying partly beneath lateral line) 16–19, 29–30 and 41–46. First and third spots may be faint or absent. There is an indication in preserved specimens that spots are ocellated, the area around them in some individuals being lighter than general background. Each scale has a small dark spot lying beneath focus, the spots are darker ventrally. Dorsum crossed by a variable number of irregular dark bars, some of which may reach lateral-line scale row. There are usually five predorsal bars (posteriormost lying just in front of dorsal origin), two bars bisected by dorsal fin, about five between dorsal and adipose fins and one posterior to adipose. These more posterior bars may be faint or absent.

Distribution

The species has been recorded from the middle and upper reaches of the Orinoco River and throughout the Essequibo River system in Guyana (Fig. 14).

Etymology

The species is named for my wife, Irina.

***Pseudanos trimaculatus* (Kner, 1859)**

Fig. 24

Schizodon trimaculatus Kner 1859:161 (original description, type locality: Mato Grosso).

Anostomus trimaculatus — Myers 1950 (partim—Peru); Géry 1961 (parts of cranial osteology, scales, teeth); Knöppel 1972 (diet).

Diagnosis

P. trimaculatus may be distinguished from *Gnathodolus*, *Sartor*, and *Synaptolaemus* by a combination of 16 circumpeduncular scales and four teeth in each lower jaw. It may be separated from striped *Anostomus* (*A. anostomus*, *A. brevior* and *A. ternetzi*) by presence of two to four rounded blotches along lateral line and narrow transverse bars across dorsum. It differs from *A. plicatus*, *A. intermedius*, and *A. spiloclistron* in cusped nature of the symphyseal lower jaw teeth (vs truncate), pelvic origin closer to the snout (\bar{x} = 51 per cent SL vs 55–56 per cent), a greater dorsal-fin origin to caudal-fin distance (\bar{x} = 55 per cent SL vs 51 per cent), a shorter snout length (\bar{x} = 38 per cent vs 43–44 per cent), a wider interorbital (\bar{x} = 38 per cent HL vs 31–33 per cent), more lateral-line scales (\bar{x} = 42 vs 39–41) and one more vertebra (\bar{x} = 39 vs 36–39) — see Table 1 — and three (vs four) branchiostegal rays. It differs from *P. gracilis* in having a deeper (\bar{x} = 26 per cent SL vs 23 per cent) and wider (\bar{x} = 14 per cent SL vs 11 per cent) body, generally having three fewer lateral-line scales (\bar{x} = 42 vs 45) and two less vertebrae (\bar{x} = 39 vs 41), presence of narrow dark transverse bars across dorsum, and an angle of 110–180° between three posterior scale radii (vs 40–90°). It can be differentiated from *P. irinae* by its usually wider body (\bar{x} = 14 per cent SL vs 13 per cent — Fig. 22), average of one less lateral-line scale (42) and vertebrae (39), and by light spots in centre of each scale (vs dark spots).

Description

A large, rather deep-bodied species (size range of material examined 51–155 mm SL), exhibiting considerable geographic variation. The following measurements are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 81.0 (77.3–87.9), 0.016, 0.002; lower jaw to adipose-fin origin 86.5 (83.1–88.7), 0.012, 0.002; lower jaw to dorsal-fin origin 49.4 (42.9–52.8), 0.015, 0.002; lower jaw to pelvic-fin origin 51.4 (47.8–57.0), 0.017, 0.002; dorsal-fin origin to caudal-fin origin 55.0 (51.6–59.5), 0.016, 0.002; dorsal-fin origin to adipose-fin origin 39.8 (33.4–44.6), 0.017, 0.002; caudal peduncle length 13.1 (11.8–15.0), 0.008, 0.001; caudal peduncle depth 10.4 (8.8–11.8), 0.007, 0.001; head length 27.7 (21.2–31.7), 0.017, 0.003; body depth 26.3 (19.2–32.7), 0.032, 0.005; body width 13.8 (10.8–16.6), 0.016, 0.003.

As percentage of head length: preopercle length 69.9 (64.1–79.9), 0.028, 0.004; snout length 37.5 (31.6–44.4), 0.024, 0.004; head depth 80.3 (60.7–99.3), 0.086, 0.012; preopercle depth 63.0 (48.8–74.4), 0.049, 0.007; snout depth 37.7 (31.6–44.1), 0.026, 0.004; eye diameter 24.4 (20.2–29.6), 0.021, 0.003; bony interorbital 38.1 (33.9–43.5), 0.018, 0.003.

Lateral-line scales 42.4 (41–44), 0.837, 0.120, dorsal transverse 5.5 (4.5–6.5), 0.411, 0.059; ventral transverse 4.5 (4–5), 0.103, 0.015; predorsal 12.3 (11–14), 0.663, 0.096; dorsal to adipose 12.8 (12–14), 0.787, 0.149; adipose to caudal 8.2 (7–10), 0.892, 0.172; isthmus to pelvis 17.1 (15–19), 1.031, 0.195; pelvis to anus 11.5 (10–13), 0.688, 0.100; anal to caudal 7.5 (6–9), 0.700, 0.135; circumpeduncular 16. Scales (from scale row above lateral line and below dorsal origin) usually with four radii (posterior three together forming an angle of about 180°). Number of radii may increase somewhat with body size, but reticulations are seldom present even in large specimens. Lateral-line scales usually with two to three (seldom four) radii, otherwise as for *P. irinae*.

Dorsal fin iii 10 (occasionally iv 9, once iv 10), caudal fin usually with 10 dorsal, 9 ventral principal rays (seldom 9 dorsal and/or 8 ventral rays), anal iii 8 (once iii 6), pelvic i 8 (twice i 7 on one side only), pectoral i 12–i 15 (\bar{x} = 13.9, SD = 0.698, SE = 0.100). Number of olfactory lamellae increasing with body size, from 22 at 48 mm SL to 36 at 102 mm SL. Vertebrae usually 39 + urostyle (\bar{x} = 39.1, range 38–41, SD = 0.704, SE = 0.182) with 12–13 (\bar{x} = 12.3) caudal including urostyle. First pterygiophore of dorsal fin inserts between neural spines of eleventh–twelfth or twelfth–thirteenth vertebrae. Three branchiostegal rays.

Teeth orange-brown, four in each half of each jaw. There is some variation in number of cusps. In upper jaw, inner (medial) two teeth bicuspid, third tooth tricuspid, outer (lateralmost) tooth with four to five cusps. In lower jaw, medial two teeth tricuspid, third tooth tricuspid (once with four cusps), lateralmost tooth with four to five cusps.

Colour in alcohol yellow-brown, paler below, with 2 to 4 dark spots along lateral line, covering scales 3 to 5 (this spot usually somewhat below, but touching, lateral line) 16–19, 29–30 and 40–44. First and third spots may be faint or absent, while second is usually ocellated with a lighter pigmentation than general background. Each scale with small light-coloured spot beneath focus. Dorsum is crossed by a variable number of irregular dark bars, some of which reach lateral line. There are about five predorsal bars (posteriormost lying just in front of dorsal-fin origin), two bars bisected by dorsal fin, about five between dorsal and adipose fins and one posterior to adipose, more posterior bars may be faint or absent. In young specimens (ca 40 mm SL) these crossbars have appearance of being formed by development of a light area in middle of a dark crossbar, edges of which remain dark and thus form two narrow bars.

Distribution

P. trimaculatus is found throughout the Amazon river system and its major tributaries (Fig. 14). It is probably this species (and not *P. irinae*) which has been found in the Rio Negro; Knöppel (1972) reports on the stomach contents of three specimens (primarily fruit with some plant remains) from this region. Ringuelet et al. (1967) report on a single specimen from Lago Itati, Corrientes River, River Paraná system of Argentina (about 28°40'S, 58°W). This is the furthest south any anostomine has been recorded.

Variation

There are some very difficult problems associated with the specimens here grouped

under *P. trimaculatus*. Grouping the specimens geographically into Mato Grosso (20 specimens), Peruvian (13; region of Nanay and Napo River mouths), Ecuadorian (13) and eastern Amazonian (5) populations, reveals fairly considerable variation. Of these, the eastern Amazon population appears to deviate most from the other three. Unfortunately only five specimens from this region were available for study and it is quite possible that these differences are more apparent than real. Graphic analysis indicates that this population has the dorsal, anal, and pelvic (Fig. 25) fins closer to the tip of the lower jaw ($R^2 = 0.92$, 0.91 and 0.97 respectively), a less deep body (Fig. 26) and head ($R^2 = 0.51$ and 0.74 respectively), shorter head length ($R^2 = 0.84$), larger eye ($R^2 = 0.87$, Fig. 23) and a longer caudal peduncle (Fig. 27, $R^2 = 0.95$). Less variation is apparent in the other populations. Specimens from the Mato Grosso have a somewhat longer snout and lower jaw-to-preopercle distance ($R^2 = 0.96$ and 0.97 respectively), while Peruvian examples have a somewhat smaller eye ($R^2 = 0.84$, Fig. 23). Peruvian and Ecuadorian specimens have a greater depth at the preopercle ($R^2 = 0.96$ for both) and a longer head ($R^2 = 0.93$ and 0.99 respectively). None of these differences is statistically significant in an analysis of variance utilizing the F-test.

Genus *Sartor* Myers and de Carvalho 1959

Sartor Myers and de Carvalho 1959:148 (type by original designation *S. respectus* Myers and de Carvalho).

Diagnosis

The genus may be recognized from all other anostomines by possession of three teeth in lower jaw (vs one or four). In common with *Gnathodolus* and *Synaptolaemus* it differs from *Anostomus* and *Pseudanos* in having a longer caudal peduncle ($\bar{x} = 16$ – 17 per cent SL vs 12 – 14 per cent), fewer vertebrae ($\bar{x} = 35$ vs 36 – 41), enlarged symphyseal teeth in lower jaw, bony part of which is longer than wide (vs subequal teeth in lower jaw which is about as long as wide) and rounded or conical dermal papillae on lower jaw. It shares with *Gnathodolus* (but not *Anostomus*, *Pseudanos* or *Synaptolaemus*) a wider body ($\bar{x} = 15$ per cent SL for *Sartor*, 28 per cent for *Gnathodolus* vs 11 – 14 per cent), and a lower jaw (bony structure minus teeth) five times as long as it is wide. *Sartor* differs from *Gnathodolus* in having a less wide body and less deep body, head and preopercle (see Table 1), as well as possessing three teeth in each half of lower jaw (vs 1). It shares with *Synaptolaemus* 12 circumpeduncular scales (vs 16 in *Anostomus*, *Pseudanos* and *Gnathodolus*).

Sartor respectus Myers and de Carvalho, 1959

Fig. 28

Sartor respectus Myers and de Carvalho 1959:149 (original description, type locality: upper Xingu River, Brazil); Géry 1961 (aspects of cranial osteology); 1972/73 (redescription from four additional specimens from upper Xingu, D'Arcy Thompson deformation coordinates); Knöppel 1972 (diet).

Diagnosis

As for genus.

Description

A somewhat compressed species (size range of material examined 60–80 mm SL), with a very narrow and elongate lower jaw. Since only three specimens were available for a study, the following counts and measurements (as percentages) are expressed as a mean followed by the range in parentheses.

As percentage of standard length: lower jaw to anal-fin origin 76.1 (75.7–76.7); lower jaw to adipose-fin origin 84.5 (83.3–85.8); lower jaw to dorsal-fin origin 49.2 (48.4–49.6); lower jaw to pelvic-fin origin 52.3 (52.0–52.7); dorsal-fin origin to caudal-fin origin 53.1 (52.8–53.3); dorsal-fin origin to adipose-fin origin 35.8 (35.7–35.9); caudal peduncle length 18.7 (18.0–20.1); caudal peduncle depth 10.8 (10.7–11.0); head length 30.0 (29.7–30.3); body depth 23.7 (22.5–25.3); body width 14.7 (14.0–16.0).

As percentage of head length: preopercle length 74.7 (72.5–76.9); snout length 43.0 (41.6–45.6); head depth 68.1 (66.9–68.8); preopercle depth 59.4 (59.0–60.3); snout depth 41.5 (40.2–43.3); eye diameter 21.3 (20.6–22.5); bony interorbital 39.3 (37.7–40.2).

Lateral-line scales 39.3 (39–40); dorsal transverse 5; ventral transverse 4; predorsal 13.3 (12–14); dorsal to adipose 11.7 (11–12); adipose to caudal 8.7 (8–9); isthmus to pelvis 17.7 (17–19); pelvis to anus 7.3 (7–8); anal to caudal 9.0 (8–10); circumpeduncular 12. Scales (from scale row above lateral line and beneath dorsal-fin origin) with up to seven radii in posterior field and five in anterior. A few reticulations at focus.

Dorsal fin iii 10, caudal with 10 upper and 9 lower principal rays, anal iii 8, pelvic i 8, pectoral usually i 16 (once i 15), Vertebrae 35 plus ural centrum, with 14 caudal (including urostyle). First pterygiophore of dorsal fin lies between neural spines of tenth and eleventh vertebrae.

Teeth four in each half of upper jaw, three in each half of lower jaw. Upper jaw teeth all bicuspid, with medial cusp larger (lateralmost tooth possibly tricuspid). Symphyseal tooth of lower jaw greatly enlarged, awllike, no cusps, a somewhat concave posterior surface, slightly recurved. It projects above the upper jaw when mouth closed. Second tooth much smaller, flattened and knifelike. Lateralmost tooth smallest, with a small lateral cusp.

Colour pattern consisting of about seven broad dark bars on a lighter background, three predorsal, one at dorsal base, two between dorsal and adipose and one at adipose. A dark spot centred on lateral line just behind adipose. Adipose black basally, translucent distally.

Distribution

At present recorded only from the upper Xingu River, Amazon River system (Fig. 8). Knöppel (1972) reports a diet of sponges and detritus, with some plant remains and larvae of ephemeropterans, trichopterans and chironomids.

Genus *Synaptolaemus* Myers and Fernandez-Yepe, in Myers 1950

Synaptolaemus Myers and Fernandez-Yepe, in Myers 1950:190 (type by original designation *S. cingulatus* Myers and Fernandez-Yepe, in Myers).

Diagnosis

Synaptolaemus may be recognized from all other anostomines in having symphyseal teeth of lower jaw about twice as long as wide (vs subequal or five times as long as broad) and having gill membranes broadly united with isthmus. It shares with *Gnathodolus* and *Sartor* (but differs from *Pseudanos* and *Anostomus*) a longer caudal peduncle (\bar{x} = 16–17 per cent SL vs 12–14 per cent), fewer vertebrae (\bar{x} = 35 vs 36–41), a lower jaw that is longer than wide (vs as long as wide) and rounded or conical dermal papillae on lower jaw. It differs from *Gnathodolus* and *Sartor* (and shares with *Pseudanos* and *Anostomus*) a narrower body (\bar{x} = 14 per cent SL vs 16–28 per cent) and a less deep preopercle (\bar{x} = 51–64 per cent HL vs 70–75 per cent) and snout (\bar{x} = 33–41 per cent HL vs 45–51 per cent) and a smaller eye (\bar{x} = 21–24 per cent HL vs 26 per cent). It shares with *Sartor* (but not *Pseudanos*, *Anostomus* or *Gnathodolus*) 12 circumpeduncular scales (vs 16).

Synaptolaemus cingulatus Myers and Fernandez-Yepe, in Myers, 1950

Fig. 29

Synaptolaemus cingulatus Myers and Fernandez-Yepe, in Myers 1950: 190 (original description, type locality: upper Orinoco near bifurcation with Casiquiare, Venezuela); Géry 1961 (aspects of cranial osteology); 1972/73 (description of upper Xingu specimens, D'Arcy Thomson deformation coordinates); Knöppel 1972 (diet).

Diagnosis

As for genus.

Description

A fusiform, somewhat compressed species, with a size range of specimens examined of 51–109 mm SL. The following measurements are expressed as percentages, and these and the meristics consist of a mean, the range in parentheses, the standard deviation and the standard error respectively.

As percentage of standard length: lower jaw to anal-fin origin 79.4 (77.7–82.0), 0.014, 0.005; lower jaw to adipose-fin origin 86.6 (84.3–88.1), 0.013, 0.005; lower jaw to dorsal-fin origin 50.7 (49.1–52.5) 0.011, 0.004; lower jaw to pelvic-fin origin 55.2 (51.7–58.4), 0.023, 0.008; dorsal-fin origin to caudal-fin origin 52.2 (50.5–53.9), 0.013, 0.005; dorsal-fin origin to adipose-fin origin 36.7 (34.8–38.3), 0.011, 0.004; peduncle length 16.8 (15.7–18.7), 0.009, 0.003; peduncle depth 10.9 (10.3–11.7) 0.006, 0.002; head length 28.5 (27.1–30.7), 0.012, 0.004; body depth 23.4 (20.8–27.2), 0.021, 0.007; body width 12.3 (9.7–14.6), 0.018, 0.006.

As percentage of head length: preopercle length 74.6 (72.3–76.7), 0.015, 0.005; snout length 43.1 (38.2–47.7), 0.035, 0.013; head depth 68.3 (64.1–75.9), 0.035,

0.012; preopercle depth 59.4 (57.0–63.4), 0.019, 0.007; snout depth 40.3 (37.6–44.0), 0.024, 0.009; eye diameter 22.4 (20.4–25.9), 0.018, 0.006; bony interorbital 27.1 (23.8–30.1), 0.022, 0.008.

Lateral-line scales 37.8 (37–39), dorsal transverse 3.5–4, ventral transverse 3–3.5, predorsal 11.0 (10–12), dorsal to adipose 11.9 (11–13), adipose to caudal 7.6 (6–9), isthmus to pelvis 15.9 (15–18), pelvis to anus 7.0 (6–8), anal to caudal 8.4 (7–10), circumpeduncular 12. Scales (from below dorsal origin) with many radii and considerable reticulations about focus (Fig. 7E). Lateral-line scales also with many radii but seldom reticulations.

Dorsal fin iii 10, caudal fin with 10 upper and 9 lower principal rays, anal iii 8, pelvic i 8 (once i 7, one side only), pectoral i 12–i 18 (\bar{x} = 15.8). Olfactory lamellae increasing with body size, from 42 at 75 mm SL to 48 at 108.5 mm SL. Vertebrae 34–35 (\bar{x} = 34.6) + ural centrum (with 13–14 (\bar{x} = 13.5) caudal vertebrae, including ural centrum. First pterygiophore of dorsal fin lies between neural spines of tenth-eleventh or eleventh-twelfth vertebrae. Four branchiostegal rays.

Four orange-brown teeth in each half of each jaw. Medial two upper jaw teeth in each jaw broadly rounded, with a somewhat irregular edge; third tooth tricuspid (with medial cusp dominating lateral ones); lateralmost tooth truncate to slightly tricuspid. In each half of lower jaw, symphyseal tooth spoonshaped (with a concave posterior surface) and nearly twice the size of next tooth, which is tricuspid. Third tooth about two-thirds size of second, and slightly tricuspid, while lateralmost tooth truncate, and very small. Upper lip finely plicate. Lower lip has four–five irregular rows of conical papillae, largest of which is about half length of exposed portion of upper jaw symphyseal pair of teeth.

Colour pattern in alcohol a darkish yellow-brown with seven light bands encircling body. Three are predorsal (third at dorsal origin), two postdorsal, one at adipose fin and one posterior to it. In life, chocolate-brown with the light bands being bright orange-red (F. Mago-Leccia, pers. comm.).

Distribution

S. cingulatus has been recorded from two localities in the Orinoco drainage system (at the bifurcation with the Casiquiare River and from the lower Paragua River) and from the upper Xingu River which drains into the Amazon near its mouth (Fig. 8). Knöppel (1972) reported that two upper Xingu specimens of *S. cingulatus* had fed extensively on ephemeropteran larvae.

Variation

The two specimens from the upper Xingu have a longer snout to pelvic fin origin (58 per cent SL vs 52–56 per cent), a greater body depth (26–27 per cent SL vs 21–24 per cent) and a deeper head (70–76 per cent head length vs 64–68 per cent) than the Orinoco population. More specimens would be needed to confirm these apparent differences.

Osteology Section

Introduction

In the following section, I have described the osteology under a series of headings encompassing convenient regions of the body. A detailed description of the bony structures in each region follows, and is derived from cleared and stained material of *Pseudanos trimaculatus*. Finally, differences from the condition described for *P. trimaculatus* are documented for all other species of anostomines for which material was available (see Appendix 2). This Variation section may consist of a single paragraph discussing all the species examined, or, where the differences are more extensive, a separate paragraph is accorded each species.

Osteological nomenclature basically follows that of Weitzman (1962) in his classic study of *Brycon*. I have departed from this nomenclature in three cases, using intercalar for his opisthotic, vomer for prevomer, and six hypurals plus a parhypural as opposed to seven hypurals. In addition, I have added, in parentheses, the more recent terminology for the bones of the lower jaw (Nelson, 1973), hyoid arch (Nelson, 1969) and occipital region (Patterson, 1975).

Infraorbital Bones and Associated Elements

Pseudanos trimaculatus

Fig. 30

Infraorbital series of six bones. Infraorbital one an elongated oval with an irregular margin, narrower posteriorly. Sensory canal bone-enclosed, in shape of an inverted "y" along anterior margin of bone. Canal openings at three extremities of "y", a fourth opening midway along shaft. Infraorbital two a more regular elongated oval with a more regular margin, sensory canal along middle of bone. Canal openings at extremities, and one roughly midway along its length. Posterior margin of infraorbital two lateral to anterior tip of infraorbital three, which has a well developed lamina ventrally. Sensory canal, open at both ends, along slightly concave dorsal margin. There may be two additional lateral openings (one anteriorly, one posteriorly). Wall of canal separating these pores from terminal openings may break down so that openings are confluent (as in figure). Infraorbital four with sensory canal passing upwards along middle of the bone. Usually a separate posterior opening dorsally, near terminal opening (not in specimen figured). Infraorbital five roughly triangular, with sensory canal along anterior margin. Infraorbital six (dermosphenotic) becoming broader posterodorsally with increasing body size. Sensory canal passing vertically upwards, along dorsal edge, resulting in a small anterodorsal lamina and a large posterior one. Dorsal portion of preopercular canal passes through posterior margin. In some individuals this canal forms posterior margin of bone, in others (e.g. figured specimen) there is a small lamina of bone posterodorsally.

Antorbital and supraorbital bones small and flat, former attached anteroventrally by connective tissue to dorsal surface of infraorbital one. Nasal flat, bearing

bone-enclosed supraorbital sensory canal. Canal straight, open at both ends, and with two lateral openings along its length.

Variation

The above description also applies to *P. irinae*. In *A. plicatus*, *A. spiloclistron* (Fig. 31A), *A. anostomus* and *A. ternetzi*, bony canal of infraorbital one is I-shaped with extended cross pieces (an "H" on its side). In *P. gracilis* and *A. intermedius* it is in form of a "less than" sign, with only three openings (Fig. 31B), in *Synaptolaemus* it is C-shaped (Fig. 32A) and in *Gnathodolus* it is Y-shaped with stem pointing anteriorly (Fig. 32B). In *Sartor*, canal is as for *A. plicatus*, etc., but posteroventral channel extends halfway along ventral margin of bone.

Infraorbital two has a better developed ventral lamina than in *P. trimaculatus* in *A. plicatus*, *A. spiloclistron* (Fig. 31A), *A. anostomus*, *A. ternetzi* and *Synaptolaemus* (Fig. 32A, where anterior portion of canal curved). In *A. intermedius* it is slightly curved anteriorly, and has an additional opening anteriorly. It is elongate in *Gnathodolus* (Fig. 32B), similar to *P. trimaculatus* in *P. gracilis* (Fig. 31B), and has an intermediate form between *Gnathodolus* and *Synaptolaemus* in *Sartor*. Infraorbital three with no significant variation. In all but *P. gracilis*, infraorbital four has a broad posterior lamina of bone (Figs. 31A, 32A, 32B).

Preopercular canal passes through posterior part of infraorbital six in *A. spiloclistron* and *A. ternetzi*. In *P. gracilis* and *A. intermedius* this canal forms extreme posterior margin of that bone, and it may be in this form or absent in *A. anostomus*. No trace of canal in *A. plicatus*, *Sartor*, *Synaptolaemus* or *Gnathodolus*. In latter two genera, infraorbital canal diverges to form two openings dorsally (Figs. 32A and 32B).

Suspensorium and Jaws

Pseudanos trimaculatus

Figs. 33, 34

Quadrate triangular, with condyle for articular anteriorly. A horizontal lateral shelf of bone, which forms floor of adductor mandibulae chamber and which continues posteriorly to end beneath anterior part of symplectic, along ventral surface of quadrate. Dorsal tip of quadrate in contact with lateral surface of palatine, notch in posterior face of quadrate. Maximum height of quadrate 35–40 per cent of its total length. Ectopterygoid small, lying along anterodorsal face of quadrate; posterodorsal process articulating with small ovoid palatine. Palatine articulates anterodorsomedially with vomer and mesopterygoid posteromedially. Mesopterygoid a small bone largely overlain laterally by metapterygoid. Metapterygoid large, upper part inclined dorsomedially to form a sloping shelf under orbit. Symplectic in contact with quadrate anteriorly, curving posterodorsally between ventral margin of the metapterygoid and preopercle. Connected to hyomandibular posterodorsally by a plug of cartilage, with interhyal articulating on medial surface of plug. Hyomandibular a vertical plate of bone lying medial to preopercle and with an anteroventral process to metapterygoid.

Opercle with a somewhat convex lateral surface and a small rounded process anterodorsally for insertion of dilatator operculi muscle. Subopercle curved, bluntly rounded. Interopercle wide posteriorly, lying lateral to anterior tip of subopercle, becoming attenuated anteriorly. Beneath anterior tip of preopercle interopercle gives rise to a long ligament to posterior face of angular. Preopercle right-angled, with a medial flange from anterior margin at angle, and lying lateral to rest of suspensorium (except for posterior extension of quadrate). Preopercle canal with a total of six openings (including terminal ones), continuing anteriorly in two small tubelike canal bones.

Maxilla flattened, with ventromedial flange beneath the posterodorsal region of the premaxilla. An anterodorsal flange covers posteroventrolateral face of premaxilla and, below this, maxilla expands into a flat, somewhat triangular plate. A nerve enters medial face of maxilla, and courses ventrally before exiting laterally. Premaxilla, when viewed from an anterodorsal position, like a right-angled triangle; a short, rounded medial flange (see Fig. 37, of *A. plicatus*) extends from ventral midline to underlie symphyseal pair of teeth. Four replacement teeth lying free in connective tissue in each jaw, underlying four functional teeth (which are attached by connective tissue). Inner three replacement teeth tricuspid, lateralmost with four to five cusps.

Articular (angulo-articular) small, forming posterior margin of lower jaw. Angular (retroarticular) very small, joined to posteroventrolateral face of jaw; coronomeckelian a small, flat, rounded bone on medial face of dentary. Dentary forming major part of lower jaw. Tooth cavity bridged medially by a thin lamina of bone (cavity thus formed being open at both ends). Replacement teeth lying free in cavity below functional teeth, with inner pair bicuspid, third tricuspid and lateralmost with four to five cusps. Inner pair of teeth (both functional and replacement) with a distinct notch across the anterior surface below cusps.

VARIATION

P. irinae. As for *P. trimaculatus*.

P. gracilis (Fig. 35). Palatine separated from quadrate by ectopterygoid. A concavity in anteroventral margin of metapterygoid; quadrate height 32 per cent its total length; otherwise as for *P. trimaculatus*.

A. plicatus (Figs. 36 and 37). Quadrate not as high as in *P. trimaculatus* (height 25–30 per cent length), lateral shelf poorly developed anteriorly. Notch in posterior face of quadrate absent; ectopterygoid (which has a very small dorsal process) separates quadrate from palatine. Sloping shelf of metapterygoid nearly horizontal. Symplectic with well-developed laminae of bone at angle, lying lateral to metapterygoid and preopercle. Posterodorsal margin of opercle somewhat concave. Ventral triangular portion of maxilla broadly expanded (see Fig. 38 of *A. spiloclistron*). Symphyseal replacement tooth of lower jaw, like functional one, without cusps, and with concave (almost spoon-shaped) posterior margin. Tooth next to it is similar, but two lateral replacement teeth have three to four cusps.

A. spiloclistron (Fig. 38). Quadrate less high than in *A. plicatus* (depth about 20 per cent of length). Metapterygoid longer than in *A. plicatus*; symplectic with small dorsal and well developed ventral bony laminae. Opercle with distinct concavity in posterodorsal surface. Symphyseal lower jaw replacement tooth without cusps, next

tooth bicuspid. Otherwise this species differs from *P. trimaculatus* as *A. plicatus* does.

A. intermedius. Quadrate narrow (depth about 21 per cent of length). Symphyseal replacement tooth of lower jaw bicuspid. Otherwise this species differs from *P. trimaculatus* in the same way that *A. plicatus* does.

A. anostomus. Quadrate depth about 28 per cent of its length, no notch in posterior edge, lateral shelf poorly developed anteriorly, quadrate separated from palatine by ectopterygoid. Metapterygoid shelf sloping. Posterodorsal margin of opercle concave. Ventral part of maxilla somewhat more developed than in *P. trimaculatus*.

A. ternetzi. Quadrate depth 25–28 per cent of its length. Ventral margin of maxilla better developed than in *A. anostomus*, with a notch in its posterior edge. Other differences from *P. trimaculatus* as for *A. anostomus*.

Synaptolaemus (Figs. 39 and 40). Quadrate height about 32 per cent of its length, quadrate separated from palatine by ectopterygoid (which has no posterodorsal process), a small notch present on posterior quadrate surface, lateral shelf from below palatine. Metapterygoid shelf sloping. Symplectic long, thin and gently curved, overlain posterodorsally by median shelf of preopercle. Opercle concave posterodorsally. Maxilla greatly expanded ventrally, nerve foramen passing straight through bone (not in a vertical channel). Premaxilla small, medial two replacement teeth without cusps, lanceolate, outer two teeth tricuspid. Lower jaw symphyseal replacement tooth without cusps, second and third tricuspid, outer without cusps.

Gnathodolus sp. (Fig. 41). Quadrate very long and thin (height 7–8 per cent length), posterior extension of lateral shelf extending to angle of preopercle, shelf beginning about midway along length of quadrate, no notch on posterior face, not in contact with palatine. Ectopterygoid long and thin, free anteriorly, no dorsal process. Palatine oblong, reaching ectopterygoid ventrally, but covered ventrolaterally by a somewhat rectangular mesopterygoid; both these bones have articular surfaces for vomer (they articulate with vomer posteroventral to lateral ethmoid). Metapterygoid shelf nearly horizontal. Preopercle ends anteriorly beneath middle of symplectic. Hyomandibular with a long, thin anteroventral process to metapterygoid. Dentary very long and narrow, only symphyseal tooth (for which two replacement teeth, one above the other, are present). Maxilla broad, foramen passing vertically through bone.

Sartor. Quadrate height 34.5 per cent of its length, separated from palatine by ectopterygoid (which has no posterodorsal process), no notch in posterior face of quadrate, lateral shelf from below palatine. Metapterygoid shelf horizontal, with a lateral extension of this shelf as well, lying dorsal to lateral shelf of quadrate. Symplectic long, thin and gently curved, overlain posterodorsally by a median process from preopercle. Opercle margin concave posterodorsally. Premaxilla small, all replacement teeth tricuspid. Foramen vertically through maxilla, which has an expanded base. Dentary elongate (but not as much as in *Gnathodolus*). Symphyseal replacement tooth without cusps, lateral two teeth bicuspid.

Hyoid Arch

Pseudanos trimaculatus

Figs. 42–44, 45B

Ventral hypohyal (ventrohyal) forming anterolateral margin of hyoid arch, with a notch in ventral surface. Dorsal hypohyal (dorsohyal) small, rounded, situated on dorsomedial surface of arch. Ceratohyal (anterohyal) large, more or less square, with a posteroventral extension. Epihyal (posterohyal) semicircular, with an anterodorsolateral foramen, joint with ceratohyal almost vertical. Interhyal small, rodlike, articulating ventrally with posterodorsolateral surface of epihyal and dorsally with medial face of cartilaginous plug separating hyomandibular and symplectic. Three spathiform branchiostegal rays; first articulating with ventral face of ceratohyal just in front of posteroventral extension, second on lateral face of this extension and third with ventrolateral face of epihyal. This latter ray has a dorsal process proximally, which is rounded in small individuals but develops into a posteriorly pointed hook in larger specimens (cf. Figs. 42 and 43). First branchiostegal ray articulates with ceratohyal by a pair of articular processes. In one Ecuadorian specimen, left lateral articulation is double, and a ridge of bone passes from point where these two lateral articulations meet along length of ray. This may indicate loss of first ray by fusion rather than reduction. Urohyal V-shaped (Fig. 44), with dorsal edge longer than ventral edge, its posterior margin variously scalloped. Basihyal rodlike, cartilaginous anteriorly. A (toothless) basihyal toothplate overlies cartilage and anterior portion of basihyal itself (Fig. 45B).

VARIATION

The above description applies to *P. irinae*, *P. gracilis* and *A. ternetzi* (but epihyal-ceratohyal joint oblique in latter). In *A. plicatus*, *A. intermedius* and *A. spiloclistron* (Fig. 46A), joint between epi- and ceratohyal is at about 45° to vertical. There are four branchiostegal rays, and urohyal is deeper and less V-shaped (Fig. 46B). *A. anostomus* (also *A. brevior*) has four branchiostegal rays, although in some individuals first ray may be considerably reduced. Epihyal-ceratohyal joint is oblique. *Synaptolaemus* (Fig. 47) with four branchiostegals; a small process on first, an anterodorsal process on second, but none on third or fourth. Foramen on dorsal surface of epihyal. Epihyal-ceratohyal joint at 35° to vertical. Urohyal with a long dorsal and much shorter ventral limb, posterior surface concave. *Gnathodolus* with four branchiostegal rays (first small), no processes. Foramen on lateral face of ceratohyal, with a long deep groove extending posteriorly onto the epihyal. Joint between epihyal and ceratohyal almost vertical. Urohyal as for *Synaptolaemus*. *Sartor* with four branchiostegal rays; a rounded process on proximal dorsal face of fourth. Foramen dorsolaterally on epihyal. Epihyal-ceratohyal joint somewhat oblique, urohyal as for *Synaptolaemus*. Basihyal toothplate with a posteriorly directed ventral hook.

Branchial Arches

Pseudanos trimaculatus

Figs. 45B, 48, 49

Basibranchials one to three present (although first not ossified in two smallest specimens), and interconnected by cartilage (Fig. 45B). Dorsally, basibranchials two and three overlain and fused to laminae of bone, which may represent toothplates. Three squarish hypobranchials, third with slightly notched surface surrounding posterior part of basibranchial three. First three ceratobranchials articulate with posterolateral margins of three hypobranchials, fourth articulates with lateral margin of median cartilaginous plug and fifth articulates with posterior face of plug. Posteromedial margin of fifth ceratobranchial expanded as a flat horizontal plate with two to three uneven rows of teeth on dorsal surface (rows passing from anteromedial to posterolateral). Seven to 10 teeth in first row, 4 to 7 in second and 0 to 4 in third. Each tooth with cusp on anterior surface proximal to tip; teeth replaced from anterior. Four epibranchials articulate with first four ceratobranchials, Y-shaped proximally (Fig. 49). Four infrapharyngobranchials, first (suspensory) rod shaped, second articulating with epibranchials one and two, third with epibranchials two and three. Fourth represented by rod of cartilage between medial face of epibranchial four and posterior face of infrapharyngobranchial three. Toothless fourth pharyngobranchial toothplate adheres to ventrolateral face of this rod of cartilage, and contacts anteromedial face of epibranchial four posteriorly. Fifth pharyngobranchial toothplate is attached to ventromedial face of fourth epibranchial; it bears two rows of teeth, cusped similarly to those on ceratobranchial five. However, here cusps face posteriorly, and teeth posteriorly replaced. Three to four teeth in anterior row and seven to eight in posterior row.

VARIATION

Both specimens of *P. irinae* lack basibranchial one (Fig. 45A). All species of *Anostomus*, and *P. irinae*, with better developed lamina on ceratobranchial five and more teeth (12–14 first row, 10–11 second row, 0–1 third row) except for *A. intermedius* which has 10–11 in first row, 4–5 in second, third row absent; more teeth on pharyngobranchial five tooth plate (4 to 8 first row, 10–12 second row) again with exception of *A. intermedius* with 1 tooth in first row and 7 to 8 in second. *Synaptolaemus* (Fig. 50) with well-developed first basibranchial, third basibranchial arched (in lateral view). Ceratobranchial five with 10 teeth in first row, then 8 to 9, and 1 in third row. Pharyngobranchial toothplate with 5 to 6 in first row, 10 in second. *Gnathodolus* with fewer teeth than other anostomines, six in first row, four in second on fifth ceratobranchial and three in first row, five in second on pharyngobranchial toothplate. *Sartor* with 13 teeth in first row of ceratobranchial five, 12 in second and 0–1 in third. Basibranchial one well developed, basibranchial series as a whole somewhat dorsoventrally flattened, third basibranchial slightly arched. Pharyngobranchial five with 7 teeth in anterior row and 12 in posterior row.

Cranium

Pseudanos trimaculatus

Figs. 51-55

Width of skull 53–57 per cent length, depth 42–46 per cent length. Ethmoid (Figs. 51–53) triangular in dorsal view, overlain by frontals posteriorly, meeting lateral ethmoids laterally and joined by cartilage to vomer ventrally. No lateral wings, bone as long as wide (width measured transversely at anterior margin of cranial fontanel, length from anterior tip to fontanel).

Vomer (Figs. 51, 52) toothless, bulbous anteriorly, becoming a laterally flattened shaft of bone sutured to parasphenoid posteriorly. Posterior to joint with ethmoid a pair of cuplike projections arise from dorsal surface to vomer, their medial edges meet in midline forming median septum. Vomer joined posterodorsally to lateral ethmoids.

Lateral ethmoid (paired) forming anterior wall of orbit (Figs. 51–53). Overlain dorsally by frontal, contacting orbitosphenoid dorsally and ventrally; these two bones enclose olfactory nerve foramen. Ventromedially lateral ethmoid joins parasphenoid (posteriorly) and vomer (anteriorly); anterodorsomedial surface contacts ethmoid. Lateral ethmoid forms posterior wall of nasal cavity. Distinct notch present in ventromedial margin for passage of olfactory nerve in small specimens; notch surrounded by thin wall of bone medially in larger individuals.

Frontal (paired) large, roofing orbit (Figs. 51, 53); contacting ethmoid anteriorly, parietal posteriorly, and lateral ethmoid, orbitosphenoid, pterospheneid, sphenotic and pterotic ventrally. Epiphyseal bars from each side meet and interdigitate in midline, as do frontals themselves in larger individuals, where a small cranial fontanel is present anteriorly. In smaller specimens anterior part of cranial fontanel open posteriorly to epiphyseal bar but in smallest specimen (43.3 mm SL, Ecuador) open for its entire length.

Parietal (paired) lying posterior to frontal, which covers it anteriorly (Figs. 51, 53); overlying pterotic laterally and epiotic and supraoccipital posteriorly. Parietals medially separated by posterior part of cranial fontanel; in large specimens, two parietals may just meet in midline anteriorly. Supraorbital and supratemporal canal systems pass through parietal.

Supraoccipital overlain by parietals anteriorly, laterally joined synchondrally to epiotic and exoccipital (Figs. 51, 53). Supraoccipital crest, and hence sulcus, short.

Exoccipital (paired) forming posteroventral face of skull (Figs. 51–54); joining other exoccipital dorsally, supraoccipital and epiotic dorsolaterally, pterotic, intercalar and prootic laterally and basioccipital ventrally. Usually a single foramen lying lateral to lagenar capsule for glossopharyngeal and vagus (IXth and Xth) cranial nerves (although one or more small foramina may be present anteriorly). Large lateral occipital foramen dorsal to lagenar capsule and lateral to foramen magnum. Floor of foramen magnum formed by a thin horizontal median lamina of exoccipital which meets a similar lamina from other exoccipital in midline; cavity formed beneath these laminae, cavum sinus imparis, in shape of a flattened ellipse.

Posttemporal fossa (Figs. 51, 53, 54) an extensive chamber on posterior face of skull, divided into dorsal and ventral portions by anterolateral arm of epiotic.

Intercalar (Fig. 52) roughly T-shaped (with posteromedial arm of "T" poorly developed). Head of "T" covers joint between pterotic and exoccipital and shaft covers junction of prootic, pterotic and exoccipital.

Basioccipital a long, narrow bone, joined to prootic anteriorly, exoccipital dorsally and parasphenoid ventrally (Figs. 51, 52, 54). Posteriorly it forms condyle for articulation of first vertebra. Baudelots ligament arises from basioccipital ventral to lagenar capsule.

Epiotic (or epioccipital; paired) contacts supraoccipital and exoccipital ventrally and medially, and pterotic ventrolaterally (Figs. 51, 53, 54). Dorsolateral face gives rise to anterior process which joins posterior face of parietal and medial process of pterotic, forming strut across posttemporal fossa.

Pterotic (paired) partly overlain dorsomedially by frontal and parietal (Figs. 51–54); contacting sphenotic anteriorly, prootic ventrally and exoccipital, intercalar and epiotic posteriorly. Well-developed ventrolateral spine-like process; no evidence of temporal foramen. Anteroventrally, pterotic has a concave depression for reception of posterior head of hyomandibular.

Sphenotic (paired) forms posterodorsal margin of orbit; covered anteriorly and medially by frontal and pterosphenoid, posteriorly by pterotic (Figs. 51–53). Behind orbit, indentation combines with frontal to form dilator fossa (overlain laterally by dermosphenotic).

Prootic (paired) large, forming major component of floor and sides of braincase (Figs. 51, 52). Contacts sphenotic, pterotic and intercalar dorsally, exoccipital and basioccipital posteriorly, parasphenoid ventrally and pterosphenoid anterodorsally. Ventromedial shelf of bone forms roof of myodome. Region of prootic-sphenotic junction concave, forming anterior part of hyomandibular fossa.

Subtemporal fossa (Fig. 52) a shallow depression mainly in pterotic, but includes posterodorsal region of prootic and rimmed posterolaterally by intercalar.

Pterosphenoid (paired) forming posterodorsal wall of orbit, partly overlain by frontals dorsally (Figs. 51, 52); contacting sphenotic posteriorly, prootic posteroventrally and orbitosphenoid anteriorly. It does not meet other pterosphenoid in ventral midline.

Orbitosphenoid (Figs. 51, 52) a more or less butterfly-shaped bone (in ventral view), joining pterosphenoid posteriorly, frontal dorsally and lateral ethmoid both dorsolaterally and anteroventromedially.

Parasphenoid a long thin bone sutured to vomer anteriorly, and joined to ventral surface of lateral ethmoid dorsally (Figs. 51, 52). A dorsolateral wing at rear of orbit is sutured to prootic but joined by cartilage behind this. Dorsal surface of posterior part of parasphenoid joined to basioccipital, a pair of flattened processes not attached to basioccipital extend posteriorly. Small ventral median keel present. Foramen present in shaft of parasphenoid below orbitosphenoid in three specimens from Mato Grosso (Fig. 55), but absent in two Ecuadorian individuals.

VARIATION

P. irinae. Width of skull 52 per cent length, depth 41–43 per cent. Foramen for olfactory nerve in lateral ethmoid completely surrounded by bone medially. Head of intercalar wider and better developed than in *P. trimaculatus*.

P. gracilis. Width of skull 55 per cent length, depth 39 per cent. Cranial fontanel

open for whole length, lateral head of intercalar well developed. Otherwise as for *P. trimaculatus*.

A. plicatus. Width of skull 52 per cent length, depth 38 per cent. Ethmoid a narrow V, its width 65 per cent of its length. Anterior tip of ethmoid hooked in lateral view. Anterior lamina of lateral ethmoid poorly developed (see Fig. 38 of *A. spiloclistron*), with a notch in its anterior margin. Foramen for olfactory nerve not walled by bone medially. Cranial fontanel entirely open. Posterior face of supraoccipital with a median ridge with a shallow groove down centre for reception of anterior face of neural complex. Sulcus wide, forming a shallow trough. Ridge of exoccipital runs from just behind the vagus foramen to head of intercalar. Joint between pterosphenoid and orbitosphenoid aligned laterally (not inclined anterolaterally). Parasphenoid keel beneath orbit well developed.

A. spiloclistron (Fig. 38). Width of skull 44 per cent length, depth 36 per cent. Cranial fontanel closed behind epiphyseal bar. Ridge behind vagus foramen present, but less well developed than in *A. plicatus*. Other differences from *P. trimaculatus* as for *A. plicatus*.

A. intermedius. Width of skull 44 per cent length, depth 37 per cent. Olfactory nerve foramen with a well-developed median wall of bone. Otherwise this species differs from *P. trimaculatus* in the same way that *A. plicatus* does.

A. anostomus (Fig. 56). Width of skull 50 per cent length, depth 33–34 percent. Ethmoid width 55–65 per cent length. Lateral ethmoid with notch in margin of poorly developed anterior lamina, olfactory foramen narrowly surrounded by bone medially. Cranial fontanel open posteriorly only to epiphyseal bar. Parietals fully joined in midline for their entire length. Supraoccipital tip exposed posterodorsally, posterior surface grooved as in *A. plicatus*, sulcus a shallow trough. Lateral exoccipital foramen well developed, ridge to intercalar posterior to vagus foramen present. Epiotic expanded dorsally, with a wide, flaring anterior process resulting in a very small dorsal chamber of posttemporal fossa. Epiotic with well-developed posterior process, posterior process of pterotic slender. Median ventral keel present on orbitosphenoid. Dorsal flange on parasphenoid ventral to anterior half of orbit, parasphenoid narrows ventral to prootic and basioccipital. No pair of free posterior processes.

A. ternetzi. Width of skull 45–50 per cent length, depth 32–35 per cent. Ethmoid a narrow V (its width 64–65 per cent of its length). Foramen for olfactory nerve open medially in two smaller specimens, but enclosed by narrow median strut of bone in largest specimens. Cranial fontanel entirely open in smaller specimen, but closed in larger example. Dorsal chamber of posttemporal fossa small (but not as reduced in *A. anostomus*) and posterior process of epiotic also less well developed. Other differences from *P. trimaculatus* are as described for *A. anostomus*.

Synaptolaemus (Fig. 57). Width of skull 45 per cent length, depth 36 per cent. Ethmoid a very narrow V (width 53 per cent length), small pair of lateral projections may be homologous with lateral ethmoid wings of *Brycon* (Weitzman, 1962). Lateral ethmoid with no anterior lamina and little indication of a notch, olfactory foramen open medially. Cranial fontanel entirely open, epiphyseal bar wide. Parietal sutured to supraoccipital at edges of posterior margin of fontanel. Supraoccipital crest a narrow V, sulcus rounded, posterior profile (in lateral view) rounded, posterior face grooved. Well-developed ridge present on exoccipital between vagus foramen and intercalar. Lateral exoccipital foramen well developed, cavum sinus imparis

rectangular. Dorsal chamber of posttemporal fossa much reduced, filled by dorsomedial expansion of epiotic. Posterior process of pterotic thin. Subtemporal fossa relatively well developed, primarily in pterotic. Pterosphenoid-orbitosphenoid joint almost vertical. Orbitosphenoid with very well-developed ventral flange, which joins process from dorsal surface of extremely well-developed dorsal flange of parasphenoid. Foramen present in parasphenoid near rear of orbit. Parasphenoid narrow beneath prootic, but widening somewhat posteriorly. Very well-developed pair of processes extending posteriorly below basioccipital condyle.

Gnathodolus sp. (Fig. 58). Width of skull 50 per cent length, depth 42 per cent. Ethmoid narrow (width 61 per cent length), no anterior lamina, notch present in anterior surface, olfactory foramen bounded by bone medially. Vomer very well developed, with short dorsolateral process to lateral ethmoid, and large, horizontal flange of bone extending a third of the way across orbit posteriorly, ventrolateral groove in posterior half of flange for articular facets of palatine and mesopterygoid. Anterior edge of palatine in line with ventrolateral process of lateral ethmoid. Cranial fontanel open. Groove in posterior face of supraoccipital and sulcus in form of shallow trough. Ridge of exoccipital from vagal foramen to intercalar well developed. Lateral occipital foramen well developed. Epiotic with narrow anterolateral process to pterotic and parietal. Dorsal chamber of posttemporal fossa large. Subtemporal fossa well-developed, no posterior process on epiotic. Joint between pterosphenoid and orbitosphenoid almost vertical. Orbitosphenoid with sharp ventral process not reaching parasphenoid. Parasphenoid with a well-developed ventral keel ending abruptly posterior to orbit; joint with vomer oblique; posterior process short.

Sartor (Fig. 59). Width of skull 59 per cent length, depth 44 per cent. Ethmoid V-shaped, its width 82 per cent of its length. Lateral ethmoid with no anterior lamina, notch on anterior face, olfactory foramen open medially. Medial keel of vomer very deep at joint with parasphenoid (similar in this respect to *Gnathodolus*). Cranial fontanel open. Sulcus wide and troughlike, posterior face of supraoccipital grooved. Ridge behind vagus well developed. Intercalar small. Dorsal chamber of posttemporal fossa well developed. No process on posterior face of epiotic. Pterosphenoid-orbitosphenoid joint oblique, orbitosphenoid with ventral flange pierced by foramina, not in contact with parasphenoid. Ventral flange of parasphenoid well developed anteriorly.

Weberian Apparatus

***Pseudanos trimaculatus* Figs. 51, 52**

First centrum simple disc of bone with pair of deep, narrow pits, one on either side of dorsal midline, which receive ventral peglike articular processes of scaphia. Second vertebra with pair of lateral processes from ventrolateral margins of centrum, the processes extend anterolaterally to anterior margin of first centrum, extending laterally until in line with (or slightly beyond) lateral margin of tripus. Neural arch pedicle of third vertebra fused to transverse process of that vertebra, transverse

process fused to anterolateral face of centrum. Dorsal and posterodorsal surfaces of neural arch pedicle contact ventral surface of neural arch complex and anteroventral surface of neural arch of fourth vertebra respectively. Pleural rib of fourth vertebra arising from a deep socket in lateral face of fourth centrum, socket roofed by a flange of bone dorsally. Rib extending laterally, lying dorsal to transformator process of tripus. Os suspensorium arising from ventral surface of rib and curving ventromedially to beneath third centrum. Os suspensoria connected together by connective tissue.

Clastrum small, curved, rodlike, passing from midline just below anteroventral tip of neural complex to posterodorsal surface of scaphium. Scaphium cup-shaped, with posterodorsal process. Peglike ventral process articulating in socket of first centrum. Scaphium joined by ligament to intercalarium. Intercalarium flat, vertical plate of bone articulating proximally between transverse process (laterally) and neural pedicle (medially) of vertebra three. Tripus complex, but basically triangular; attached anteriorly via ligament to posterolateral face of intercalarium. Triangular body of tripus a flat, horizontal lamina of bone, with raised dorsal ridges along two proximal edges. Anterior of these ridges split vertically from proximal apex of triangle for much of length of ridge. More medial of double ridges so formed continues medially, firmly bound into deep socket in vertebra three, and forming a leaf-springlike suspension for tripus. Posterolateral margin of tripus gives rise to thin transformator process which curves posteromedially (ventral to pleural rib of vertebra four) to end just posterior to ventral tip of os suspensorium (being connected to latter by a fan-shaped ligament). Neural complex a broad flat lamina of bone attached to posterior face of cranium anteroventrally and to dorsal faces of neural pedicle and neural spine of third and fourth vertebra ventrally.

VARIATION

The description above also applies to *P. irinae* and *P. gracilis*. In *A. plicatus*, *A. spiloclistron* and *A. intermedius* transverse process of vertebra three with a foramen, anterior process of os suspensorium well developed, neural complex narrow dorsally, and "leaf-spring" suspension of tripus less well developed. *A. anostomus* and *A. ternetzi* with better-developed transverse process on vertebra two and narrow neural complex; in latter species, pleural rib of vertebra four expanded dorsally and anteriorly, overlying posterior region of tripus. In *Synaptolaemus* (Fig. 60) transverse process of vertebra two curving posterodorsally, and that of vertebra three passing out laterally (as opposed to anterolaterally). Neural pedicle of vertebra three less well developed. Pleural rib of vertebra four with anterodorsal flange overlying tripus, and lateral process curving anterolaterally. This latter condition also found in *Sartor*, but not in *Gnathodolus*. In all three genera dorsal part of neural complex narrow.

Pectoral Girdle

Pseudanos trimaculatus

Figs. 61, 62

Extrascapular a small flat bone connected to anterolateral face of posttemporal and bearing semicircular sensory canal on its medial face, posterior surface of which gives rise to two other canals. Posttemporal a thin lamina of bone with a short medial process near its ventral margin with sensory canal passing horizontally across it just beneath medial process. Large foramen in middle of this canal giving rise to posteroventrally directed canal passing through dorsal tip of supracleithrum. Supracleithrum with shallow fork dorsally. A canal running ventrally in supracleithrum to exit laterally near medial margin of that bone. Three postcleithra; dorsalmost small, ovoid, closely applied to posteroventromedial margin of supracleithrum; postcleithrum two a long flat lamina of bone attached to posteromedial face of cleithrum; postcleithrum three (ventralmost) rodlike, attached to anteroventromedial margin of postcleithrum two.

Cleithrum large, attached to mesocoracoid medially, scapula dorsomedially, and coracoid at two points anteroventromedially. Cleithrum with long, tapering dorsal process and broad, triangular posterior lamina just above fin rays. Mesocoracoid a vertical strut between coracoid (dorsally) and V-shaped joint with scapula (posteriorly) and coracoid (anteriorly); at dorsal end a thin strut of bone passing posterolaterally along medial face of cleithrum. Coracoid joined to cleithrum in two places anteroventrally, to mesocoracoid dorsally and scapula posterodorsally; supporting ventralmost proximal radial (IV) posteriorly. Scapula somewhat curved bridge of bone between cleithrum (dorsally), mesocoracoid (anteroventrally) and coracoid (ventrally), supporting three dorsal proximal radials posteriorly (dorsalmost of which (I) largest). Eight distal radials, dorsalmost three supported by dorsalmost proximal radial (I).

VARIATION

P. irinae and *P. gracilis* have posteroventral margin of sensory canal in supracleithrum Y-shaped, with two openings. This applies to all other anostomines except *Synaptolaemus*, *Gnathodolus* and some individuals of *A. ternetzi*, where single. In all these other species, joint between mesocoracoid and scapula and coracoid is ✓-shaped rather than V-shaped. Postcleithrum one reduced in *A. spiloclistron*, absent on one side but present on other in single specimen of *A. intermedius*, separated from postcleithrum 2 and reduced in *Gnathodolus*, and absent in *Synaptolaemus* and *Sartor*. In *Synaptolaemus* ten distal radials and four proximal radials in close contact with one another. Six distal radials present in *Gnathodolus*, eight in *Sartor*.

Pelvic Girdle

Pseudanos trimaculatus

Figs. 63, 64

Pelvic bone (paired) a long, narrow sheet of bone, tapering to point anteriorly. Medial process on the dorsal surface sutured to process from opposite side in midline. Ischial process arises from posteroventral surface, passing posteriorly and then posterodorsally. Ridge present on ventral face of pelvis which forms large, lateral articular surface for radials and lateralmost fin rays. Four radial elements, lateral two paired, third and fourth single. Third small, lying at posterodorsolateral margin of fourth. Fourth very well developed consisting of globular base with a flat, posterior process lying medial to dorsal half of innermost fin ray. It is possible (and even probable) that the large fourth radial represents the dorsal half of the small third radial, thus there would be three paired radials in each pelvic fin.

VARIATION

In *P. irinae*, *Synaptolaemus* and *Sartor*, pelvic bones tend to be joined rather than sutured in midline (*Gnathodolus* not examined).

Dorsal and Anal Fins

Pseudanos trimaculatus

Figs. 65, 66

Eleven proximal pterygiophores in dorsal fin (Fig. 65), vertical plates of bone with thin laminae on anterior and posterior edges. Medial pterygiophores lie posterodorsal to third to last proximal pterygiophores. Eleven distal pterygiophores (paired) present. Anteriormost 3 (unbranched) fin rays articulate with first proximal and distal pterygiophores, other 10 fin rays articulate each with its own distal pterygiophore. Posteriormost fin ray is split through its base. Posterior to last proximal pterygiophore a flat rounded piece of bone, the end piece or stay of Weitzman (1962).

VARIATION

In *P. irinae* dorsal stay absent. First four proximal pterygiophores of *A. plicatus* and *Synaptolaemus* lack medial pterygiophores; *A. spiloclistron*, *A. intermedius* and *P. gracilis* lack first three, *Sartor* lacks first two, *A. anostomus* lacks first four to five and *A. ternetzi* lacks first three to six.

In anal fin, nine proximal pterygiophores similar in shape to those of dorsal fin (Fig. 66). Medial pterygiophores present posteroventral to third through ninth proximal pterygiophores. Nine distal pterygiophores (paired) present, first proximal and distal pterygiophores support first three (unbranched) fin rays. Posteriormost ray split through its base: anal stay present. In large specimens, third proximal and medial pterygiophores may be fused. Small paired nubbin of bone (=unbranched ray?) may be present in front of first unbranched ray (Fig. 66).

The above applies to *P. gracilis*, *P. irinae*, *A. spiloclistron*, *A. intermedius* and *Synaptolaemus*. *A. plicatus* has medial pterygiophores present from fifth proximal pterygiophore, *A. anostomus* from fourth to fifth, *A. ternetzi* from second to fifth and *Sartor* from second. *P. irinae*, *P. gracilis*, *A. anostomus* and *A. ternetzi* usually have small paired nubbins of bone anterior to first unbranched fin ray.

Caudal Skeleton

Pseudanos trimaculatus

Fig. 67

Four upper and two lower hypurals. Upper hypurals fit against posteroventral surface of urostyle. Dorsalmost of lower hypurals fused anteriorly to compound ural centrum, lowermost well removed from centrum. Parhypural fused to ventral surface of ural centrum. Two pairs of uroneurals, anterior pair being much larger, lying parallel to, and on either side of urostyle. Well-developed anterior flange (or modified neural process) present on anterodorsal face of urostyle, notched dorsally for reception of three epurals (of which second largest). Tip of neural spine of second preural centrum (pu 2) supports dorsal procurent rays and tips of haemal spines of pu 2 and pu 3 support ventral procurent rays. Modified neural process bifid in one specimen from Ecuador.

VARIATION

Above description applies to *P. irinae*, *P. gracilis* and *A. ternetzi* (in one specimen of latter, neural spine of pu 2 is half normal size). In *A. plicatus*, *A. spiloclistron*, and *A. intermedius* a foramen present in lowermost hypural, uroneural 1 wider and better developed, and a large anterior lamina present on neural spine of pu 2. In *A. anostomus*, uroneural 2 absent (present on one side of one specimen as a single minute nubbin of bone).

DISCUSSION

Interpretation of the osteological data (as well as dermal papillae and colour pattern) is based on the belief that Hennig's (1966) method of phylogenetic reconstruction is, at the present time, the most logical and consistent (and thus most useful). The approach to the analysis of information is similar to that adopted in an earlier paper (Winterbottom 1974b). In attempting to elucidate the phylogenetic relationships within the Anostominae, I have examined three other genera of anostomid characoids (*Abramites*, *Leporinus* and *Schizodon*), and have utilized the osteological studies of Roberts (1969, 1974) and Weitzman (1962, 1964) on other groups of characoids in my efforts to establish character states and trends. All osteological characters which exhibited variation in the Anostominae were subjected to analysis. In some cases, I could not obtain any interpretable results, usually because I was unable to find any basis for decisions on whether a given character condition was primitive or derived. A selection of these cases is discussed below. However, comparison of the various conditions of a character found in the anostomines with the condition of that character in other anostomids, as well as other characoids, frequently allowed parsimonious

interpretations as to the direction of the transformation series (i.e. relative apomorphy/plesiomorphy of each condition) of that character.

The data are analysed under the same anatomical headings as used in the descriptive section.

Infraorbital Bones

INFRAORBITAL 1

In many generalized characoids, the sensory canal of this bone is straight and has three openings, the terminal ones, and one at its midlength. I find it extremely difficult to hypothesize the primitive arrangement of this canal in the anostomids, but it would appear to have been a single tube, possibly curved, with a total of four openings (as in *Abramites* and *Schizodon*). Variation in canal pattern in anostomines is considerable, and I find it impossible to erect any one hypothesis that appears to be more plausible than any other hypothesis. This also applies to the other infraorbitals, but the condition of the sixth infraorbital (or dermosphenotic) warrants some consideration (see below).

INFRAORBITAL 6

Usually this bone carries the infraorbital canal, which branches into two canals dorsally. This condition is met in, for example, *Brycon* (a characid; Weitzman, 1962), *Leporinus*, *Schizodon*, *Gnathodolus* and *Synaptolaemus*. In other anostomines, and in *Abramites*, the dermosphenotic is broadly developed posteriorly (rather like the condition figured for *Hepsetus* and *Hoplias* by Roberts, 1969). In *Hepsetus*, *Hoplias* and *Abramites* the canal is branched dorsally. This is not the case in *Sartor*, *Anostomus* and *Pseudanos*; the canal is not branched dorsally. In the latter two genera, and in *Abramites* (but with the exceptions of *Anostomus plicatus* and some specimens of *A. anostomus*), the dorsal portion of the preopercular sensory canal passes vertically across the posterior border of the dermosphenotic. Once again it is difficult to arrive at any plausible hypothesis of relationship without *a priori* assumptions. If two canals passing through the dermosphenotic is an advanced condition, *Abramites* is more closely related to the genera *Pseudanos* and *Anostomus* (with, presumably, the exception of *A. plicatus* and some specimens of *A. anostomus*) than either is to *Gnathodolus*, *Sartor* or *Synaptolaemus*. Alternatively, if an unbranched infraorbital canal is advanced, then *Sartor*, *Pseudanos* and *Anostomus* are sister groups, and the presence of the preopercular canal in the dermosphenotic is due to convergence. It seems reasonable to assume that the ancestor of *A. plicatus* possessed this canal, and that its presence or absence in *A. anostomus* is due to reduction rather than incipient development. Even given this assumption, though, the quandary remains.

Suspensorium and Jaws

QUADRATE-METAPTERYGOID FENESTRA

This is a primitive feature for many characoids, including *Abramites*, *Leporinus* and *Schizodon*. It is very much reduced or totally absent in all anostomines. (Traces of it

are present in *Synaptolaemus* and *P. gracilis*.) Thus it is probable that the common ancestor of the anostomines possessed only a rudimentary quadrate/metapterygoid fenestra.

PALATINE-QUADRATE RELATIONSHIPS

In most characoids, the palatine and quadrate bones are well separated, but in all anostomines they are very close to each other and, in two species, *P. trimaculatus* and *P. irinae*, they are actually in contact. This would indicate that the anostomines are monophyletic (derived from a form which was specialized relative to other anostomids in the close approximation of the palatine and quadrate). Additionally, the actual contact of these two bones in *P. trimaculatus* and *P. irinae* would suggest that they are sister groups.

QUADRATE

In all the anostomids I have seen, or of which I have seen figures (e.g., in Géry, 1961, Figs. 11, 17–20, which include *Anostomoides*, *Laemolyta* and *Rhytiodus* among those I have not personally examined), the ventral margin of the quadrate is expanded laterally to form a flattened or slightly curved longitudinal shelf or trough. The shelf begins near the articular condyle of the quadrate, and is produced posteriorly beyond the rear margin of the main body of that bone. This shelf is complete in the species of *Pseudanos* but reduced or absent anteriorly in the remaining anostomines. Thus it would seem that the lateral shelf was reduced in a common ancestor of *Sartor*, *Synaptolaemus*, *Gnathodolus* and *Anostomus*.

ECTOPTERYGOID

A dorsal process arises from the posterior margin of the ectopterygoid in all anostomids examined, with the exception of the three monotypic anostomine genera (where this condition would appear to be advanced and indicates that they are monophyletic).

METAPTERYGOID

In most characoids, the metapterygoid is a vertical sheet of bone. In all anostomines, the dorsal portion of the metapterygoid either slopes medially or, in *A. plicatus*, *A. spiloclistron*, *A. intermedius*, *Sartor* and, to a lesser extent, *Gnathodolus*, it forms a flat, almost horizontal shelf dorsally. From the structure of this shelf, the horizontal nature in *Sartor* and *Gnathodolus* may or may not be homologous with that of the *A. plicatus* group, but the character is difficult to interpret further. If it is homologous it would indicate that the genus *Anostomus* is paraphyletic. The fact that the shelf is inclined medially in anostomines provides evidence consistent with the hypothesis that the Anostominae is monophyletic.

MAXILLA

The toothless maxilla of anostomids is usually a thin, curved rod of bone. In all anostomines except *Pseudanos* the ventral portion of the maxilla is expanded into a flat triangular plate, indicating these forms share a common ancestor.

OPERCLE

Another character with this distribution is the posterodorsal margin of the opercle, which is straight in *Abramites*, *Leporinus*, *Schizodon* and *Pseudanos* but concave in all other anostomines. This is another indication that the forms with a concave margin to the opercle are monophyletic.

Hyoid Arch

BRANCHIOSTEGAL RAYS

The species of *Pseudanos*, together with *A. ternetzi* and *Abramites*, have three branchiostegal rays. All other anostomids I have seen have four. The implication here is that these forms share a common ancestor which had three branchiostegal rays and, since the first branchiostegal of *A. anostomus* is frequently much reduced in size, that these forms are the sister group of *A. anostomus*. This interpretation is at variance with the hypothesis of relationships presented here, based on analysis of all the available evidence (see p. 49 et seq.). A posterior process on the last branchiostegal ray is present in all anostomids examined except *Gnathodolus*, *Sartor* and *Synaptolaemus*, indicating that these three genera form a monophyletic unit.

EPIHYAL-CERATOHYAL JOINT

The joint is vertical in *Pseudanos*, *Abramites*, *Leporinus* and *Schizodon*, slightly oblique in the monotypic genera and at about 45° to the vertical in members of *Anostomus*. This transformation series suggests a common ancestor for the monotypic genera plus *Anostomus* with a slightly oblique epihyal-ceratohyal joint. The common ancestor of the species of *Anostomus* subsequently increased the angle of the joint to 45° from the vertical, indicating the monophyletic nature of the genus.

UROHYAL

The urohyal is a broad V-shaped bone in all anostomids seen, except in *A. plicatus*, *A. intermedius* and *A. spiloclistron*, where it is very high dorsally, and indicative of the common ancestry of these three species.

Cranium

ETHMOID

All anostomines except *Pseudanos* have a narrow ethmoid (width 53–82 per cent of length vs width equal to length in the species of *Pseudanos* and 1.07–1.30 times length in the other anostomids examined). This is evidence consistent with the hypothesis that *Anostomus* and the monotypic genera form a monophyletic group. In *A. plicatus*, *A. intermedius* and *A. spiloclistron* the anterior tip of the ethmoid is hooked, indicating a common ancestor with this condition.

LATERAL ETHMOID

The lateral ethmoid of *Abramites*, *Leporinus*, and *Schizodon* has no notch in its

anteroventral margin and is well developed; it is even better developed in *Pseudanos*. In all other anostomines the lateral ethmoid is very poorly developed and there is a distinct notch in the anteroventral margin immediately above the lateral ethmoid-ectopterygoid ligament. The implications here are that both conditions represent synapomorphies. The species of *Pseudanos* represent a monophyletic group since they shared a common ancestor with a very well-developed lateral ethmoid; the other anostomines form a monophyletic group because their common ancestor possessed a poorly-developed, notched lateral ethmoid.

SUPRAOCCIPITAL

All anostomids examined except *Pseudanos* have the posterior surface of the supraoccipital grooved in the midline for reception of the neural complex of the Weberian apparatus. This is indicative of the monophyletic nature of the genus *Pseudanos*. This relationship of the species of *Pseudanos* is further evidenced by the narrow supraoccipital sulcus which has a distinct rim around. Other anostomines and anostomids possess a broad, gradual sulcus with no distinct rim.

EXOCCIPITAL-INTERCALAR RIDGE

Abramites, *Leporinus*, *Schizodon*, and *Pseudanos* have a flat area on the exoccipital between the vagus foramen and the intercalar. In all other anostomines, a distinct ridge of bone is present between these two points. The parsimonious interpretation is that these other anostomines shared a common ancestor which possessed the ridge.

PTEROSPHEOID-ORBITOSPHEOID JOINT

The joint between the pterospheoid and the orbitospheoid in *Abramites*, *Leporinus*, *Schizodon*, and *Pseudanos* passes out laterally, almost at right angles to the axis of the body. The joint is slightly more anteriorly inclined in *Sartor*, and more so in the other anostomines (passing from anterolateral to posteromedial); however, this character is difficult to quantify.

PARASPHEOID

Amongst characoids in general, the paraspheoid quite often forms a thin strut across the floor of the orbit. This condition is also found in the three anostomid genera examined. It is dorsoventrally extended in *Pseudanos* and in all other anostomines, and indicates that the subfamily is monophyletic.

Weberian Apparatus

NEURAL COMPLEX

In the species of *Pseudanos*, the neural complex is a broad flat sheet of bone dorsally (as opposed to a narrow rod dorsally in anostomids and other anostomines), indicating that the species of *Pseudanos* form a monophyletic assemblage.

Pectoral Girdle

MESOCORACOID JOINT

In anostomids, *Anostomus* and the monotypic genera, the mesocoracoid is joined primarily to the coracoid. The species of *Pseudanos* are thus apparently specialized in that the joint is about equally shared by the scapula and coracoid.

Caudal Skeleton

HYPURAL FORAMEN

Anostomus plicatus, *A. spiloclistron*, and *A. intermedius* all possess a foramen in hypural one. I have not seen this elsewhere in anostomids or other anostomines, and it would appear to be a synapomorphy.

NEURAL SPINE

The above three species share the presence of an enlarged lamina of bone on the anterior face of the neural spine of pu 2 not found in other anostomines or anostomids. This condition apparently represents another synapomorphy.

Two further characters are of interest here. The three monotypic genera possess conical or rounded dermal papillae on the lower lips, which I have not seen elsewhere among characoids. The second character involves colour patterns. I have found analysis of these patterns impossible without making *a priori* assumptions of character state. Whichever assumption one makes as to the primitive colour pattern of these fishes, the subsequent interpretations involve reversals of hypothesized trends of evolution and, further, postulates of convergence. For example, the anostomid genus *Leporinus* contains species with both striped (e.g. *L. striatus*) and barred (e.g. *L. fasciatus*) colour patterns, although I hasten to add that I know of no unequivocal evidence that *Leporinus* constitutes a monophyletic group. No purpose would be served by speculation on anostomine colour pattern at this point, especially when juveniles less than 30 mm SL are not available (so that possible colour changes with growth could be detected to aid in formulation of hypotheses of character state change).

The subfamily Anostominae appears to share the following osteological specializations not found elsewhere in the family: the very close proximity or contact between the palatine and the dorsal surface of the quadrate; a sloping or horizontal metapterygoid shelf; the reduction or loss of the metapterygoid-quadrate fenestra, an ethmoid which is as long or longer than wide (see osteological description for definition of measurements); and a parasphenoid which possesses a vertical lamina or keel of bone and is thus more than a simple strut across the orbit. (This character, while apparently unique to the anostomines among the anostomids, is not unique among characoids generally.)

I assume the following character states to be specialized within various lineages of the Anostominae, and provide the evidence consistent with the phylogenetic tree presented as Figure 68.

BRANCH POINT 1

Pseudanos possesses six specializations which indicate its monophyletic nature:

- i) the anterior lamina of the lateral ethmoid is very well developed and is not notched;
- ii) the posterior face of the supraoccipital is not grooved for the reception of the anterior edge of the neural complex;
- iii) the supraoccipital sulcus is narrow and steep-sided, with a distinct rim around the edge;
- iv) the dorsal portion of the neural complex is broad in lateral view;
- v) the mesocoracoid is jointed equally to the scapula and coracoid; and
- vi) there are three branchiostegal rays (but see *Ansotomus ternetzi*, which also has three).

Subjectively, I consider characters v) and vi) weak, that is, quite possibly subject to convergence.

The lineage containing the three monotypic genera and *Anostomus* share eight osteological specializations, which provide evidence that they comprise a monophyletic assemblage:

- i) the lateral shelf of the quadrate is incomplete anteriorly;
- ii) the maxilla is expanded into a triangular process ventrally;
- iii) the posterodorsal surface of the opercle is concave;
- iv) the epihyal-ceratohyal joint is inclined at an angle to the vertical;
- v) the ethmoid is longer than it is wide;
- vi) there is a ridge of bone on the exoccipital between the vagus foramen and the intercalar;
- vii) the joint between the pterosphenoid and orbitosphenoid is more obliquely inclined; and
- viii) the anterior lamina of the lateral ethmoid is poorly developed, but has a well-developed notch in its leading edge.

Of these, I feel characters ii), iii), iv), and vii) to be weak.

BRANCH POINT 2

Pseudanos trimaculatus and *P. irinae* are extremely similar in morphology and most of the differences between them and *P. gracilis* appear to be due to specializations in the latter (i.e. autapomorphies). The former two species are apparently specialized in that they are the only anostomids in which the palatine and quadrate are in contact. If this is valid, it would imply that dark spots in the centres of the scales is a primitive character for the genus, since this colour pattern is found only in *P. irinae* and *P. gracilis*.

BRANCH POINT 3

The monotypic genera (*Gnathodolus*, *Sartor*, and *Synaptolaemus*) share the following specializations:

- i) no dorsal process on the ectopterygoid;
- ii) loss of the dorsal process on branchiostegal ray four (i.e. the posterodorsalmost ray);
- iii) conical dermal papillae on the lips of the lower jaw;

- iv) symphyseal lower jaw teeth at least twice as long as the teeth next to them; and
- v) a lower jaw (bony structure) longer than wide.

The genus *Anostomus* has three possible specializations to separate it from the monotypic genera. The 45° angle of the ceratohyal-epihyal joint appears to be unique. The second infraorbital is well developed, and the quadrate height is less than 30 per cent of its length. The former is subjective, and the latter seems to be negated by *Gnathodolus*, where the quadrate height is 7–8 per cent of its length. However, given the very trenchant specializations shared by *Gnathodolus* and *Sartor* (see Branch Point 4), the bizarre nature of the jaw suspension in the former, and the fact that the latter and *Synaptolaemus* have a quadrate height of 32–35 per cent of its length, the condition in *Gnathodolus* would seem to be uniquely derived. I therefore think it extremely unlikely that any species of *Anostomus* is more closely related to the stem of the monotypic genera than it is to the other species of that genus.

BRANCH POINT 4

I suggest that *Gnathodolus* and *Sartor* are more closely related to each other than either is to *Synaptolaemus* because of the following specializations:

- i) an extremely elongate and narrow lower jaw;
- ii) the loss of one (*Sartor*) or three (*Gnathodolus*) of the lateral lower jaw teeth;
- iii) the great elongation of the symphyseal lower jaw tooth; and
- iv) the very deep median flange on the vomer and parasphenoid.

Set against this is the fact that *Sartor* and *Synaptolaemus*, uniquely among anostomines, have 12 circumpeduncular scales (vs 16). Although this appears to be an important character, I do not consider it sufficiently “powerful” to offset the specializations outlined above linking *Sartor* and *Gnathodolus*. Given the extensive and incredible cranial modifications of *Gnathodolus*, it is not too illogical to suggest that the 16 circumpeduncular scales in this genus are the result of atavism, a phenomenon certainly not without apparent precedent in fishes (see, e.g., Winterbottom, 1974b:77, 78). The problem, at least at present, is that atavism is an untestable hypothesis.

BRANCH POINT 5

The genus *Anostomus* seems clearly divided into two groups of three species each; *A. plicatus*, *A. spiloclistron* and *A. intermedius* on the one hand and the striped species (*A. anostomus*, *A. brevior* and *A. ternetzi*) on the other. Specializations in the former group are:

- i) symplectic with dorsal and ventral laminae of bone developed in the region of the angle;
- ii) ethmoid hooked anteriorly;
- iii) symphyseal teeth of lower jaw truncate in individuals larger than 60 mm SL;
- iv) a very deep urohyal;
- v) foramen present in hypural one; and
- vi) broad lamina on anterior face of neural spine of pu 2. The second species group has a less-deep skull (32–35 per cent of its length) and is unique among anostomines (but not anostomids) in having a striped colour pattern. It may also be specialized in having more teeth on ceratobranchial 5 and on the fifth pharyngobranchial toothplate, but this needs confirmation. The evidence for the monophyletic nature of the striped

species thus seems tenuous, but given that the genus *Anostomus* and the three monotypic genera represent not only a monophyletic group, but are together the sister group of *Pseudanos* (where evidence is stronger) it seems extremely probable that the striped colour pattern is, in fact, a synapomorphy.

BRANCH POINT 6

The evidence linking *A. plicatus* and *A. spiloclistron* is very weak. My decision has been based on the more consistently truncate nature of the symphyseal lower jaw teeth, the fact that the replacement teeth for the symphyseal teeth are truncate (bicuspid in *A. intermedius* and cusped in most anostomids), and because these two species have vertical pigmented areas below the lateral line. The latter character may not represent a synapomorphy. In overall view, the external morphological similarities are between *A. plicatus* and *A. intermedius* while the osteological similarities are between *A. plicatus* and *A. spiloclistron*. However, similarities *per se* are not useful in phylogenetic analysis.

BRANCH POINT 7

Since no specimens of *A. brevior* were available for osteological study, the hypothesized relationship is extremely tentative. In most of the morphometrics, *A. ternetzi* and *A. brevior* appear to diverge in opposite directions from an *A. anostomus*-like bauplan. If, as has been hypothesized under Branch Point 5, the stiped colour pattern is an advanced character for the Anostominae, then it would seem reasonable to postulate that complete stripes are more advanced than intermittent (dorsal) stripes. It is on this basis alone that this section of the phylogeny is tentatively based.

I have not subdivided the subfamily up into tribes, subtribes, etc., (which would certainly be possible at this stage) because I believe that there are many other as yet undescribed species of anostomines in the freshwaters of South America. Their discovery could create hierarchical problems if a detailed hierarchical classification were offered at this time. Instead, I have chosen to follow the intermediary procedure outlined by Winterbottom (1974b). This system, involving the use of numerical suffixes, allows the phylogenetic relationships of the contained hierarchical units to be read off from the formal classification and at the same time permits each hierarchical category to contain more than two subcategories. It has the additional advantage that any newly discovered form can be fitted into the existing system without necessarily having to change the hierarchical levels, the new phylogenetic information being reflected in the changes in the numerical suffixes. To prevent any possibilities of confusion, I hasten to add that this is not numerical taxonomy.

Subfamily: Anostominae.

Genus: *Pseudanos*

Species: *P. gracilis* 1

P. trimaculatus 1.1

P. irinae 1.1

Synaptolaemus

S. cingulatus 2

Sartor

S. respectus 2.1

Gnathodolus

G. bidens 2.1

Anostomus

A. intermedius 3

A. plicatus 3.1

A. spiloclistron 3.1

A. ternetzi 4

A. anostomus 4.1

A. brevior 4.1

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Literature Cited

COCKERELL, T.D.A.

- 1914 The scales of South American characinid fishes. *Annals of the Carnegie Museum* 9:92–113.

CUVIER, G. and A. VALENCIENNES.

- 1849 *Histoire naturelle des poissons*. Vol. 22, Paris.

EIGENMANN, C.H.

- 1912 The freshwater fishes of British Guiana, including a study of the ecological groupings of species, and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum* 5:11–578.

FERNANDEZ-YEPEZ, A.

- 1949 *Anostomus ternetzi* nuevo anostomido de Sur America, colectado en Palital, Estado Guarico, Venezuela. *Boletin de la Sociedad Venezolana de Ciencias Naturales* 11:293–295.

FOWLER, H.W.

- 1906 Further knowledge of some heterognathus fishes. Part I. *Proceedings of the Academy of Natural Sciences of Philadelphia* 58:293–351.
- 1943 A collection of fresh-water fishes from Colombia, obtained chiefly by Brother Nicéfero Maria. *Proceedings of the Academy of Natural Sciences of Philadelphia* 95:223–266.
- 1945 Colombian zoological survey. Part I — The freshwater fishes obtained in 1945. *Proceedings of the Academy of Natural Sciences of Philadelphia* 97:93–135.

GÉRY, J.

- 1960 Contributions à l'étude des poissons characoides (No. 14). Révision de la super-espèce *Anostomus anostomus* (L.) et description de formes nouvelles: *A. brevior* et *A. anostomus longus* (Erythrinidae, Anostominae). *Bulletin du Muséum National d'Histoire Naturelle*, 2e sér., 32:498–505.
- 1961 Contributions à l'étude des poissons characoides 13. Structures et évolution des Anostominae. *Bulletin of Aquatic Biology* 2:93–112.
- 1972/73 Notes sur quelques Anostomidae (Pisces, Characoidei) du bassin Amazonien. *Vie et Milieu* 23:143–175.
- 1977 Characoids of the world. New Jersey, Tropical Fish Hobbyist. 672 pp.

- GISTEL, J.
1848 *Naturgeschichte des Tierreichs für höhere Schulen.* Stuttgart.
- GREENWOOD, P.H., D. E. ROSEN, S. H. WEITZMAN and G. S. MYERS.
1966 Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* 13:341–455.
- GRONOW, L.T.
1754–1756 *Museum Ichthyologicum. Lugduni Batavorum.* 2 vols.
1763 *Zoophylacii Gronoviani fasciculus primus exhibens animalia quadrupeda, amphibia atque pisces, quae in museo suo adservat, rite examinavit, systematics disposuit, descripsit atque iconibus illustravit. Laurentius Theodorus Gronovius. Lugduni Batavorum.*
1854 Catalogue of fish collected and described by L. T. Gronow, now in the British Museum, ed. by J. E. Gray. London. 196 pp.
- HENNIG, W.
1966 *Phylogenetic systematics.* Chicago, University of Illinois Press. 261 pp.
- KNER, R.
1859 Zur Familie der Characinae. III. Folge der Ichthyologischen Beiträge. *Denschriftender Kaiserlichen Akademie der Wissenschaften* 17:136–182.
- KNÖPPEL, H.A.
1972 Zur Nahrung tropischer Süßwasserfische aus Südamerika. *Amazoniana* 3:231–246.
- LINDBERG, G.U.
1974 *Fishes of the world.* New York, John Wiley. 545 pp.
- LINNAEUS, C.
1758 *Systema naturae.* 10th ed. Holmiae.
- LOWE, R.H. (McCONNELL)
1964 The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *Journal of the Linnean Society (Zoology)* 45:103–144.
- MAGO-LECCIA, F.
1970 Lista de los peces de Venezuela, incluyendo un estudio preliminar sobre la ictiogeografía del País. Caracas, Ministerio de Agricultura y Cria, Oficina Nacional de Pesca. 283 pp.
- MYERS, G.S.
1927 Descriptions of new South American fresh-water fishes collected by Dr. Carl Ternetz. *Bulletin of the Museum of Comparative Zoology* 68:107–135.
1950 Studies on South American fresh-water fishes. II. The genera of anostomine characids. *Stanford Ichthyological Bulletin* 3: 184–198
- MYERS, G.S. and A. L. de CARVALHO.
1959 A remarkable new genus of anostomine characid fishes from the upper Xingu in central Brazil. *Copeia* (1959): 148–152.
- NELSON, G. J.
1969 Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History* 141:475–552.
1973 Relationships of clupeomorphs, with remarks on the structure of the lower jaw of fishes. *In* Greenwood, P.H., R. S. Miles, and C. Patterson, eds., *Interrelationships of fishes.* London, Academic Press, pp. 333–349.
- PATTERSON, C.
1975 The braincase of pholidorhynchid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 269:275–579.

RAFINESQUE, C.S.

- 1815 Analyse de la nature, ou tableau de l'univers et des corps organisés. Palerme. 224 pp.

RAMIREZ, E.M.V.

- 1957 Nuevas especies para la fauna ictiologia Venezolana. Boletin de la Sociedad Venezolana Ciencias Naturales 18:157-162.

RINGUELET, R.A., R. H. ARAMBURU, and A. A. de ARAMBURU.

- 1967 Los peces Argentinos de Agua dulce. La Plata, Buenos Aires Gobernacion, Comision de Investigation Cientifica. 602 pp.

ROBERTS, T.R.

- 1969 Osteology and relationships of characoid fishes, particularly the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenolucius*, and *Acestrorhynchus*. Proceedings of the California Academy of Sciences, 4th Ser., 36:391-500.
- 1974 Osteology and classification of the neotropical characoid fishes of the families Hemiodontidae (including Anodontidae) and Parodontidae. Bulletin of the Museum of Comparative Zoology 146:411-472.

SCOPOLI, G.A.

- 1777 Introductio ad historiam naturalem. Prague. 506 pp.

STEINDACHNER, F.

- 1882 Beiträge zur Kenntniss der Flussfische Südamerika's. ii. Beschreibungen von 51 Fisch-Arten. Denkschriftender Akademie Wissenschaften zu Wien 43:103-146.

SWAINSON, W.

- 1839 The natural history and classification of fishes, amphibians and reptiles, or monocardian animals. London. 2 vols.

WEITZMAN, S.H.

- 1962 The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin 8:1-77.
- 1964 Osteology and relationships of South American characid fishes of subfamilies Lebiasininae and Erythrininae with special reference to the subtribe Nannostomina. Proceedings of the United States National Museum 116:127-170.

WINTERBOTTOM, R.

- 1974a A new species of anostomid characoid fish, *Anostomus spiloclistron*, from the Nickerie river system of western Surinam (Pisces, Cypriniformes, Anostomidae). Beaufortia 21:153-163.
- 1974b The familial phylogeny of the Tetraodontiformes (Pisces: Acanthopterygii) as evidenced by their comparative myology. Smithsonian Contributions to Zoology 155:1-201.

Appendix I. List of Material Examined

Anostomus anostomus

GUYANA. AMNH 7086, 2, 56.3–93.1 mm SL, Essequibo River system, Potaro River at Erukin Creek; coll: C. H. Eigenmann, 1908. AMNH 8225, 1, 100.8 mm SL, Kurupung River (tributary of Mazaruni River ?); coll: H. Lang. AMNH 17601, 1, 59.6 mm SL, Essequibo River system, Kuyuwini River; coll: R. Snedeger, Dec. 2, 1937. AMNH 17648, 2, 57.7–85.1 mm SL, Essequibo River system, Kuyuwini River, between mouth and Marudi Creek; coll: R. Snedeger, Dec. 9, 1937. AMNH 31027, 4, 36.1–56.0 mm SL, Demerara River, 1934. AMNH 31030, 4, 42.0–107.0 mm SL, Demerara River System, at Wismar. Aug. 1935. AMNH 31031, 40, 40.1–75.7 mm SL, Demerara River system at Wismar, 1934. BM(NH) 1911-10-31-462, 81.0 mm SL, Essequibo River system at Crab Falls; coll: C. H. Eigenmann, Oct. 31, 1911. BM(NH) 1936.44: 15–16, 2, 41.2–59.8 mm SL, Demerara River system at Wismar; coll: Pinkus, Apr. 4, 1936. BM(NH) 1972.10.17: 1466, 1, 89.4 mm SL, Essequibo River system. Potaro River at Amatuk, swamp/creek; coll: R. Liley, Oct. 17, 1972. CAS 15777, 3, 59.6–87.7 mm SL, Essequibo River system, Potaro River at Erukin. CAS 15778, 2, 67.4–72.5 mm SL, Essequibo River system, Potaro River at Tumatumari. CAS 15780, 2, 45.7–68.8 mm SL, Essequibo River system at Crab Falls. CAS 15781, 1, 84.5 mm SL, Essequibo River system, Potaro River, creek below Potaro landing. FMNH 7316, 1, 66.3 mm SL, Essequibo River System at Crab Falls; coll: C. H. Eigenman, 1908. FMNH 50161, 3, 78.8–86.8 mm SL, Corantienne River system, New River; coll: E. R. Blake, Oct. 1938. FMNH 53384, 2, 49.2–74.3 mm SL, Essequibo River system at Crab Falls; coll: C. H. Eigenmann, 1908. FMNH 53385, 2, 51.3–76.7 mm SL, Essequibo River System, Potaro River at Tumatumari; coll: C. H. Eigenmann, 1908. FMNH 53386, 1, 78.3 mm SL, Essequibo River system, Potaro River at Potaro landing; coll: Shideler, 1908. FMNH 53387, 1, 71.4 mm SL, Essequibo River system, Potaro River at Kangaruma; coll: Shideler, 1908. FMNH 53388, 2, 51.0–97.2 mm SL, Essequibo River system, Potaro River, Erukin Creek; coll: C. H. Eigenmann, 1908. FMNH 53389, 1, 57.8 mm SL, Essequibo River system, Potaro River at Amatuk; coll: C. H. Eigenmann, 1908. FMNH 69600, 2, 69.4–73.6 mm SL, Essequibo River system, Potaro River at Potaro landing; coll: C. H. Eigenmann, 1908. MCZ 29921, 1, 85.3 mm SL, Essequibo River system at Crab Falls; coll: C. H. Eigenmann. SU 21772, 1, 71.1 mm SL, Essequibo River system at Crab Falls; coll: C. H. Eigenmann, 1908. ZMA 102.227, 1, 71.1 mm SL, Essequibo River system, Potaro River at Erukin Creek; coll: C. H. Eigenmann, 1908.

PERU. ANSP 112491, 1, 93.5 mm SL, Amazon River system, Concordia, coastal parts of lower Nucuray River into Marañón River; coll: Manuel, Oct. 1958. MNHN 1961–1128, 2, 91.6–102.4 mm SL (paratypes of *A. a. longus*). Amazon River system, confluence of Nucuray and Marañón Rivers near Concordia; coll: Manuel, Oct. 1958.

SURINAM. RMNH 18497, 1, 88.9 mm SL, Saramacca River system, upper Saramacca River at Toegoemoetoe; coll: de Kok Exped., Feb. 15, 1903. RMNH 18498, 1, 90.5 mm SL, data as above; coll: de Kok Exped., Feb. 9, 1903. RMNH uncat., 8, 69.6–82.6 mm SL, Corantijn River system, Kabelebo River, tributary below Avanovero Falls; coll: M. Boeseman, Apr. 6, 1971. RMNH uncat., 8,

71.0–86.1 mm SL, data as above; coll: M. Boeseman, Apr. 10, 1971. RMNH uncat., 1, 55.9 mm SL, Suriname River system, Sara River, Kurambaolo Creek above dam; coll: M. Boeseman, Dec. 22, 1963. RMNH uncat., 1, 84.5 mm SL, Tapanahoni, 2.5 km downstream from Palomeu Airport; coll: G. F. Mees, Nov. 30, 1965. RMNH uncat., 1, 68.3 mm SL, Suriname River at Brokopondo; coll: M. Boeseman. RMNH uncat., 2, 72.5–93.2 mm SL, Suriname River system, rapids at Brokopondo; coll: M. Boeseman. RMNH uncat., 1, 80.0 mm SL, Suriname River system, 1–2 km from outlet of Gran (=Marowijne) Creek; coll: M. Boeseman. RMNH uncat., 2, 72.2–81.2 mm SL, Suriname River system, Gran Creek 12 km above outlet; coll: M. Boeseman. RMNH uncat., 2, 64.5–68.0 mm SL, Saramacca River system, stagnant pool below Feddiprati Rapids; coll: M. Boeseman. RMNH uncat., 2, Suriname River system, tributary of Gran Creek near shore of Brokopondo Lake; coll: M. Boeseman. ZMA 105.293, 4, 47.6–76.6 mm SL, Suriname River system. Marowijne Creek, rotenone, sand bottom to 1.5 m; coll: H. Nijssen, Oct. 20, 1966. ZMA 105.407, 1, 83.9 mm SL, Suriname River system, Gran Rio 2.5 km NE of Awaradam, rotenone, 2 m wide, 100 cm deep, sand bottom; coll: H. Nijssen, Jan. 28, 1967. ZMA 105.418, 4, 80.2–90.6 mm SL, Suriname River system, Gran Rio 4 km NE of Awaradam, rotenone, 6 m wide, 1.5 m deep, sand bottom; coll: H. Nijssen, Jan. 31, 1967. ZMA 105.450, 8, 67.4–88.9 mm SL, Suriname River system, Gran Rio 1 km N of Dombaai, rotenone, 5 m wide, 1 m deep, sand and mud bottom; coll: H. Nijssen, Jan. 30, 1967. ZMA 105.526, 4, 62.5–94.2 mm SL, Coppename River system, rotenone, 4 m wide, 1.5 m deep, sand and rock bottom; coll: H. Nijssen, May 9, 1967. ZMA 105.527, 1, 82.6 mm SL, Coppename River system, rotenone, 5 m wide, 1 m deep, rock and sand bottom; coll: H. Nijssen, May 10, 1967. ZMA 106.529, 8, 49.7–81.2 mm SL, Coppename River system, 4 m wide, 1 m deep, sand and mud bottom; coll: H. Nijssen, May 18, 1967. ZMA 106.530, 7, 63.5–89.7 mm SL, Coppename River System, rotenone, 5 m wide, 2 m deep, sand and mud bottom; coll: H. Nijssen, May 19, 1967. ZMA 105.595, 2, 73.8–79.3 mm SL, Saramacca River system, Kleine Saramacca River 14 km ESE of mouth, rotenone, 80 m wide, 2 m deep, sand bottom; coll: H. Nijssen, Feb. 28, 1967. ZMA 105.600, 3, 71.5–75.9 mm SL, Saramacca River system, Toebaka Creek near Kleine Saramacca mouth, rotenone, 4 m wide, 1 m deep, sand and mud bottom with branches; coll: H. Nijssen, Mar. 2, 1967. ZMA 105.651, 4, 70.0–87.1 mm SL, Saramacca River system, creek on Kleine Saramacca River 13 km ESE from mouth, rotenone, 3 m wide, 1 m deep, sand and rock bottom, stagnant; coll: H. Nijssen, Feb. 28, 1967. ZMA 105.668, 1, 62.5 mm SL, Saramacca River system, Kleine Saramacca River 11 km ESE of mouth, rotenone, 4 m wide, 1 m deep, sand and rock bottom; coll: H. Nijssen, Feb. 27, 1967. ZMA 105.780, 32, 61.5–90.3 mm SL, Suriname River system, Awara Creek, rotenone, 8 m wide, 1.5 m deep, sand bottom; coll: H. Nijssen, Mar. 18, 1967. ZMA 105.789, 2, 51.7–72.5 mm SL, Suriname River system, 1 km S of Botopasi, rotenone; coll: H. Nijssen, Mar. 22, 1967. ZMA 105.799, 13, 73.0–89.9 mm SL, Suriname River system, Parwapa Creek 2.5 km N of Botopasi, rotenone, 8 m wide, 2 m deep, sand bottom; coll: H. Nijssen, Mar. 20, 1967. ZMA 106.524, 3, 65.1–93.8 mm SL, Suriname River system, Jenjee Creek 7.5 km N of Botopasi, rotenone, 3 m wide, 1.2 m deep, sand bottom; coll: H. Nijssen, Mar. 21, 1967. ZMA 106.525, 1, 56.0 mm SL, Suriname River system 7.5 km N of Botopasi at rapids, rotenone, rock bottom; coll: H. Nijssen, Mar. 21, 1967. ZMA 106.528, 25, 47.7–84.4 mm SL, Coppename River system near

Wilhelmina Mtns, rotenone, 15 m wide, 4 m deep, sand bottom; coll: H. Nijssen, May 17, 1967.

VENEZUELA. SU 16187, 1, 43.5 mm SL, Orinoco River system, rapids between Atabapo and D'Autures; coll: C. Ternetz, April, 1925. SU 16274, 2, 46.6–52.2 mm SL, Venezuela, Orinoco River system, bifurcation with Casiquiare River at Laja Tama Tama; coll: C. Ternetz, Mar. 26, 1925.

Anostomus brevior

FRENCH GUIANA. MNHN 01-405, 1 (holotype), 86.5 mm SL, French Guiana, Oyapok River system at its junction with the Camponi (= Camopi?) River. Coll: Geay, 1901. MNHN 01-406/409, 4 (paratypes), 69.1–81.5 mm SL, data as for holotype.

Anostomus intermedius

BRAZIL. Holotype: SMF 10651, 77.7 mm SL, Brazil, Amazon River system, upper Xingu River, below the cataracts near Suya-Missu or Paranajuba; coll: H. Schultz, Nov. 15, 1960.

Paratypes: BM(NH) 1977.1.7:1, 74.5 mm SL, collected with the type. SMF 13618, 14, 49.0–92.0 mm SL, collected with the type. USNM 216593, 78.7 mm SL, collected with the type.

Anostomus plicatus

GUYANA. As for Winterbottom (1974a), consisting of AMNH 17602, 17605, 17610, 17646 and the following paratypes: CAS 27647, 27648, 27649, 27650, FMNH 53394, 53395 and 53396, all 12 specimens being from the Essequibo River system.

Anostomus spiloclistron

SURINAM. As in Winterbottom (1974a), consisting of ZMA 112.685 (holotype) and ZMA 105.776, ZMA 105.777, ANSP 124334, CAS 27725 and USNM 209432 (paratypes), all 16 specimens being from near the Stondansi Falls, Nickerie River.

Anostomus ternetzi

I have not examined the types of this species. A holotype and single paratype are in the collections of the Museo de Ciencias Naturales de Caracas, Venezuela (numbers 46.001 and 46.002 respectively).

BRAZIL. MZUSP 5161, 2, 36.8–37.2 mm SL, Amazon River system, Surumu River at Surumu (junction with Branco River); coll: Alvarenga, Oct., 1966. MZUSP 9989, 3, 64.4–74.0 mm SL, Amazon River system, Tapajós River, Igarapé Apéu (Boa Vista, Para.); coll: P. E. Vanzolini, Feb. 3–4, 1964. MZUSP 9990, 12, 60.3–90.1 mm SL, Paná River system, Capim River near mouth at Belém do Pará; coll: R. Takase. SMF 10650, 10, 46.3–64.7 mm SL, Amazon River system, upper Rio Xingu, below cataracts near Suyo Missu (or Paranajuba); coll: H. Schultz, 15 Nov., 1960. SMF 10653, 5, 46.2–60.9 mm SL, data as above.

GUYANA. AMNH 17650, 1, 71.7 mm SL, Terry-Holden Expedition, 1937–1938. ANSP 39788-90, 3, 64.1–73.6 mm SL, Essequibo River System, Rupununi River; coll: J. Ogilvie, 1912. BM(NH) 1861-1.2.21:90, 1, 56.8 mm SL, Essequibo River system; coll: Ehrhardt, Jan. 2, 1864. BM(NH) 1972-7.27:127-128, 2, 46.9–53.7 mm SL, Essequibo River system, Rupununi River, Simoni Creek at Tacupas, just north of

Karenambo; coll: R. H. Lowe-McConnell, May, 1961. BM(NH)1972-7-27:129, 1, 76.5 mm SL, Essequibo River system, Manar stop-off; coll: R. H. Lowe-McConnell. BM(NH) 1972-7-27:130, 1, 64.5 mm SL. Essequibo River system, Rupununi River at Karenambo; coll: R. H. Lowe-McConnell. BM(NH) 1972-7-27:131, 1, 44.4 mm SL, Essequibo River System, Rupununi River, Moreby Creek; coll: R. H. Lowe-McConnell. BM(NH) 1972-7-27:132-133, 2, 54.1-67.9 mm SL, Essequibo River system, Rupununi River, Arakwais Creek; coll: R. H. Lowe-McConnell.

SURINAM. RMNH uncat., 3, 53.2-56.0 mm SL, Marowijne River system, upper Tapanohoni River, rotenone; coll: G. F. Mees, Nov. 27, 1965. RMNH uncat., 2, 56.1-100.2 mm SL, Marowijne River system, Tapanohoni River 2 km downstream from Paloemeu River mouth; coll: G. F. Mees, Nov. 17, 1965.

VENEZUELA. CAS 20093, 1, 56.9 mm SL, Orinoco River system, rapids between Atabapo and D'Autures; coll: C. Ternetz, Apr. 1925. CAS 20094, 1, 62.0 mm SL, Orinoco River system at Caicara; coll: C. Ternetz, May 1, 1925. CAS 20095, 4, 48.7-71.0, Orinoco River system at bifurcation, Tama Tama rocks; coll: C. Ternetz, Mar. 26, 1925. SU 60681, 2, 44.9-51.6 mm SL Orinoco River system, Orinoco River at Kiratare; coll: C. Ternetz, Mar. 30, 1925.

Gnathodolus bidens

VENEZUELA. CAS 20087, (holotype), 108.8 mm SL, Casiquiare River at Chemoni (near the bifurcation with the Orinoco); coll: C. Ternetz, Mar. 18, 1925. CAS 27651, (paratype), 73.4 mm SL, Orinoco River System at Laja Tama Tama (near bifurcation with the Casiquiare River); coll: C. Ternetz, Mar. 24, 1925. MCZ 31566, (paratype), 88.3 mm SL, collected with CAS 27651.

Pseudanos gracilis

BRAZIL. NMV 57-119, 1 (holotype), 69.2 mm SL, Amazon River system, Guaporé River; coll: Natterer, 1832-1837. BM(NH) 1912-9-4-11, 1, 47.9 mm SL, Amazon River system, Rio Negro at Manaus; coll: Arnold, Sept. 4, 1912.

VENEZUELA. CAS 20105, 4, 86.2-136.4 mm SL, Orinoco River system, mouth of Atabapo River at San Fernando; coll: C. Ternetz, Apr. 8, 1925. CAS 20107, 1, 95.8 mm SL, Orinoco River system, mouth of Atabapo River at San Fernando; coll: C. Ternetz, Apr. 8, 1925. CAS 20108, 2, 45.7-51.2 mm SL, Orinoco River system, rapids at Chorro Salata; coll: C. Ternetz, Apr. 16, 1925. CAS 20111, 1, 66.0 mm SL, Orinoco River system at Kiratari; coll: C. Ternetz, Mar. 30, 1925. SU 16275, 1, 74.2 mm SL, Orinoco River system, at Kiratari; coll: C. Ternetz, Mar. 30, 1925. SU 16276, 2, 41.1-106.6 mm SL, Orinoco River system, rapids at Chorro Salata; coll: C. Ternetz, Apr. 16, 1925. SU 16277, 1, 115.7 mm SL, Orinoco River system, Cucuhy, San Carlos de Rio Negro; coll: C. Ternetz, Feb. 22, 1925. SU 16278, 1, 152.5 mm SL, Orinoco River system, mouth of Atabapo River at San Fernando; coll: C. Ternetz, Apr. 9, 1925. SU 16279, 1, 150.2 mm SL, Orinoco River system, bifurcation with Casiquiare River at Laja Tama Tama; coll: C. Ternetz, Mar. 24, 1925. SU 16280, 7, 68.0-160.5 mm SL, Orinoco River system, mouth of Atabapo River at San Fernando; coll: C. Ternetz, Apr. 7-8, 1925. SU 54602, 1, 79.5 mm SL, Orinoco River system, mouth of Cãno de Quiribana at Caicara; coll: C. Ternetz, May 13, 1925.

Pseudanos irinae

GUAYANA. Paratypes: AMNH 14359, 1, 71.3 mm SL, Essequibo River system at Rockstone; coll: Pinkus Expedition, March, 1938. AMNH 17612, 20, 66.8–100.3 mm SL, Essequibo River system, Rupununi River just below Yupukarri near Maranambo (McTurk's ranch); coll: R. Snedeger (Terry-Holden Expedition), 1937–38. BM(NH) 1911-10-31-463, 1, 53.6 mm SL, Essequibo River system at Crab Falls; coll: C. H. Eigenmann, 31 Oct., 1911(?). BM(NH) 1972.7.27. 125–126, 2, 63.3–71.3 mm SL, Essequibo River system, Rupununi River, Crane Pond at Maranambo; coll: R. H. Lowe-McConnell, 27 Jul., 1972. FMNH 53390, 1, 97.1 mm SL, Twoca Pan; coll: Grant, 1908. FMNH 53391, 1, 71.0 mm SL, Essequibo River system at Crab Falls; coll: C. H. Eigenmann, 1908. FMNH 53392, 1, 56.0 mm SL, Essequibo River system at Rockstone; coll: C. H. Eigenmann, 1908. FMNH 53392, 1, 56.0 mm SL, Essequibo River system at Rockstone; coll: C. H. Eigenmann, 1908.

VENEZUELA. Holotype: SU 58809, 70.6 mm SL, Orinoco River system, Orinoco River at bifurcation with Casiquiare River, Laja Tama Tama; coll: C. Ternetz, 24 Apr., 1925.

Paratypes: CAS 15771, 1, 73.3 mm SL, Orinoco River System, Caño de Quiribana to Orinoco; coll: C. Ternetz, 13 May, 1925. CAS 15787, 1, 78.8 mm SL, Monagas Province, ?Acio Queribana. CAS 20097, 10, 60.9–75.4 mm SL, Orinoco River system, Orinoco River at bifurcation with Casiquiare River, Laja Tama Tama; coll: C. Ternetz, 20 Apr., 1925. CAS 20098, 6, 68.1–92.6 mm SL, Orinoco River system, Orinoco River at Caño de Quiribana; coll: C. Ternetz, 13 May, 1925. CAS 20100, 1, 61.5 mm SL, Orinoco River system at Carcara; coll: C. Ternetz, 1 May, 1925. SU 16281, 9, 59.5–77.0 mm SL, Orinoco River system, Orinoco River at bifurcation with Casiquiare River, at Tama Tama Rocks and Lake; coll: C. Ternetz, 20–26 Apr., 1925. SU 16282, 1, 77.2 mm SL, Casiquiare River at Buenavista; coll: C. Ternetz, 1 Feb., 1925. SU 68303, 2, 75.7–75.9 mm SL, collected with the holotype.

Pseudanos trimaculatus

BRASIL. FMNH 69596, 19, 47.7–92.5 mm SL, Amazon River system, Guaporé River at Maciel; coll: Haseman, Jul. 30, 1909. FMNH 69598, 1, 59.3 mm SL, Amazon River system at Santarem, south bank just downstream from junction of Amazon and Tapajos Rivers; coll: Haseman, Dec. 15, 1909. MCZ 20444, 1, 64.2 mm SL, Amazon River system at Obydos (=Obidos); coll: Thayer Expedition. NMV 2692, 1 (holotype), 155.2 mm SL, Mato Grosso. USNM 209430, 3, 61.2–77.5 mm SL, Para River system, Capim River near mouth, at Belém do Para; coll: J. R. Axelrod, Nov. 1963.

ECUADOR. BM(NH) 1970.4.3.33-44, 11, 40.7–106.7 mm SL, Jatuncacha, Amazon River system, Napo River at Lake Jatun (=Jatuncacha); coll: D. Kershaw, 1969.

PERU. ANSP 137593, 1, 69.3 mm SL, Amazon River drainage, Rio Nanay at Loreto (vicinity of Iquitos) well above Morana Creek and 14 km from the Amazon, tenone; coll: M. Horn, Oct. 19, 1955 (Catherwood Expedition). ANSP 137594, 4, 67.4–67.8 mm SL, data as above. ANSP 137595, 1, 62.1 mm SL, locality as above; coll: C. G. Chaplin & party, Oct. 14, 1955 (Catherwood Expedition). BM(NH) 1968.8.12.30:1, 1, 71.5 mm SL, Amazon River drainage, Rio Nanay near mouth, north of Iquitos; coll: R. Heath, Dec. 30, 1968. CAS 15774, 2, 55.4–59.5 mm SL, Amazon River system at Iquitos; coll: P. S. Morris, 1922. SU 16284, 2, 77.7–102.3 mm SL, Amazon River system, Ampiyacu River near Pebas (?); coll:

W. G. Scherer, Jul. 25, 1941. SU 36917, 1, 101.3 mm SL, locality as above; coll: W. G. Scherer, Sept. 10, 1937. USNM 175912, 1, 67.6 mm SL, locality as above; coll: W. G. Scherer, Jan. 18, 1935.

Sartor respectus

I have not seen the holotype of this species, which is in the collection of the Museum Nacional, Rio de Janeiro. There are no paratypes.

BRAZIL. SMF 10652, 3, 60.0–87.7 mm SL, Amazon River system, upper Xingu below cataracts near Suyu Missu (or Paranajuba); coll: H. Schultz, Nov. 15, 1960.

Synaptolaemus cingulatus

BRAZIL. SMF 10222, 2, 51.1–77.6 mm SL, Amazon River system, upper Xingu, below cataracts near Suyu Missu (or Paranajuba); coll: H. Schultz, 15 Nov., 1960. VENEZUELA. CAS 2014, 3 (paratypes), 75.0–108.5 mm SL, Orinoco River system, Orinoco River at Laja Tama Tama (at bifurcation with Casiquiare River); coll: C. Ternetz, Mar. 24, 1925. MBUCV V-4252, 2, 71.2–90.0 mm SL, Orinoco River system, Rio Paragua, Auraima Rapids (State of Bolivar), rock bottom, rotenone, 25°C; coll: J. Moscó and A. Machado, Oct. 7, 1966. SU 16122, 1 (holotype), 70.1 mm SL, Orinoco River system, upper Orinoco River at Laja Supira; coll: C. Ternetz, Apr. 6, 1925.

Appendix 2. Cleared and Stained Material

Note: In the figure legends, catalogue numbers and sizes of specimens are given only where ambiguity might otherwise arise.

Anostomus anostomus

3, 74.0–79.5 mm SL, RUSI 5522. No data (aquarium specimens).

Anostomus brevior

No material.

Anostomus intermedius

1 (paratype), 69.2 mm SL, SMF 13618, Brazil, upper Xingu River.

Anostomus plicatus

1, 73.5 mm SL, AMNH 17602, Guyana, Essequibo River.

Anostomus spiloclistron

1 (paratype), 82.5 mm SL, ZMA 105.777, Surinam, Nickerie River.

Anostomus ternetzi

2, 60.3–86.0 mm SL, MZUSP 9990, Brazil, Para River.

Gnathodolus sp.

1, 51.5 mm SL, BM(NH) 1972.12.5:5, aquarium specimen.

Pseudanos gracilis

1, 91.3 mm SL, SU 16280, Venezuela, Orinoco River.

Pseudanos irinae

1 (paratype), 74.0 mm SL, CAS 20097, Venezuela, Orinoco River. 1 (paratype), 66.2 mm SL, SU 16281, Venezuela, Orinoco River.

Pseudanos trimaculatus

2, 43.3–71.6 mm SL, BM(NH) 1970.4.3:33-44, Ecuador, Napo River. 3, 52.1–86.0 mm SL, RUSI 5521, Brazil, Guaporé River (ex FMNH 69596).

Sartor respectus

1, 65.7 mm SL, SMF 10657, Brazil, upper Xingu River.

Synaptolaemus cingulatus

1, 71.2 mm SL, MBUVC V-4252, Venezuela, Paragua River.

COMPARATIVE MATERIAL OF OTHER ANOSTOMIDS

Abramites hypselonotus

2, RUSI 5523, Brazil, Santerem.

Leporinus reinhardti

2, RUSI 5526, Brazil, San Francisco River.

Leporinus striatus

2, RUSI 5525, Bolivia, Cerro del Amboro.

Schizodon isognathus

1, RUSI 5524, Brazil, Bastos.

Appendix 3. Gazetteer of Localities Mentioned in the Text

Note: Where only the name of a river is given, the coordinates listed are at the mouth of that river.

BRAZIL

Belém do Pará	1°27'S, 48°29'W
Guaporé River	11°55'S, 65°02'W
Igarapé Apéu	3°23'S, 55°30'W
Manaus	3°06'S, 60°00'W
Obidos	1°52'S, 55°30'W
Paranajuba	11°22'S, 53°09'W
Santarem	2°26'S, 54°41'W
Surumu	3°24'N, 60°20'W
Suyu Missu	11°22'S, 53°09'W

ECUADOR

Jatuncacha (Lake)	1°05'S, 75°27'W
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FRENCH GUIANA

Camponi (=Camopi?)	3°12'N, 52°17'W
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GUYANA

Amatuk	5°18'N, 59°18'W
Crab Falls	5°24'N, 58°57'W
Crane Pond	3°46'N, 59°18'W
Demerara River	6°46'N, 58°10'W
Erukin Creek	5°20'N, 59°16'W
Kangaruma	5°17'N, 59°10'W
Karanambo	3°46'N, 59°18'W
Kurupung River	6°14'N, 60°10'W
Kuyuwini River	2°14'N, 58°19'W
Marudi Creek	2°15'N, 58°12'W

New River	3°19'N, 57°32'W
Potaro Landing	5°20'N, 59°05'W
Rockstone	6°00'N, 58°30'W
Rupununi River	4°02'N, 58°32'W
Tacupas	3°45'N, 59°17'W
Tumatumari	5°17'N, 58°59'W
Twoca Pan	4°02'N, 58°32'W
Wismar	5°58'N, 58°36'W
Yupukarri	3°40'N, 59°21'W

PERU

Ampiyacu River	3°20'S, 71°50'W
Iquitos	3°51'S, 73°13'W
Loreto	3°40'S, 73°15'W
Nucuray River	4°55'S, 75°32'W

SURINAM

Avanovero Falls	4°49'N, 57°24'W
Awara Creek	4°15'N, 55°27'W
Botopasi	4°14'N, 55°27'W
Brokopondo	5°05'N, 55°04'W
Coppename River	3°51'N, 56°00'W
Gran Creek	5°34'N, 55°07'W
Gran Rio	4°05'N, 55°37'W
Jenjee Creek	4°17'N, 55°25'W
Kleine Saramacca River	4°58'N, 55°33'W
Kurambaolo Creek	4°30'N, 54°57'W
Marowijne Creek	5°34'N, 55°07'W
Paloemeu River	3°21'N, 55°26'W
Parwapa Creek	4°15'N, 55°26'W
Stondansi Falls	5°09'N, 56°29'W
Tapanahoni	4°22'N, 54°27'W
Toeboek Creek	5°00'N, 55°34'W
Toekoemoetoe	4°12'N, 55°54'W
Wilhelmina Mountains	3°49'N, 56°57'W

VENEZUELA

Atabapo	4°03'N, 67°45'W
Auraima Rapids	6°17'N, 63°35'W
Buenavista	1°58'N, 66°42'W
Caicara	7°38'N, 66°10'W
Caño de Quiribana	7°38'N, 66°10'W
D'Autres	8°37'N, 62°15'W
Laja Tama Tama	3°08'N, 65°52'W
San Carlos de Rio Negro	1°54'N, 67°06'W
San Fernando	4°03'N, 67°45'W
Tama Tama Rocks	3°08'N, 65°52'W

Upper figure represents the mean, with the range (rounded to the nearest whole number) in parentheses below.

Species	Percentage of Standard Length					Percentage of Head Length			Meristics	
	Pelvic Origin	Dorsal Caudal	Head Length	Peduncle Length	Peduncle Depth	Snout Length	Head Depth	Interorbital	Lateral Line	Vertebrae
<i>A. anostomus</i> n = 212	52.2 (49-56)	52.8 (47-57)	26.5 (23-32)	11.6 (9-15)	10.7 (9-13)	41.0 (36-46)	66.2 (50-80)	32.8 (30-36)	39.3 (38-43) usually 39-40	36.2 (35-39) + ural
<i>A. brevior</i> n = 5	51.1 (50-52)	53.4 (52-54)	25.5 (25-26)	13.2 (13-14)	11.1 (10-12)	39.8 (38-41)	81.4 (79-85)	34.5 (34-36)	38.6 (38-39)	36.2 (36-37)
<i>A. intermedius</i> n = 17	56.7 (55-59)	50.7 (49-52)	30.1 (28-32)	13.1 (12-14)	11.9 (11-12)	40.1 (39-42)	74.8 (71-84)	32.9 (30-35)	38.9 (38-40)	35.9 (35-37)
<i>A. plicatus</i> n = 12	56.1 (53-60)	50.9 (48-53)	29.3 (27-32)	13.8 (13-16)	11.8 (11-12)	43.9 (41-47)	76.3 (71-82)	32.8 (29-36)	38.6 (38-39)	35.6 (35-36)
<i>A. spiloclistron</i> n = 15	55.1 (54-57)	51.3 (49-53)	29.1 (27-31)	11.5 (11-13)	11.6 (11-12)	42.8 (42-45)	69.1 (63-82)	31.3 (30-34)	41.0 (40-42)	37.6 (37-38)
<i>A. ternetzi</i> n = 38	51.9 (48-54)	52.8 (51-55)	26.0 (24-30)	13.9 (10-16)	10.2 (9-11)	40.3 (34-44)	61.5 (54-69)	31.6 (29-34)	40.2 (39-42)	37.3 (37-38)
<i>G. bidens</i> n = 3	51.8 (49-53)	55.0 (54-57)	30.6 (30-31)	16.0 (15-17)	13.3 (13-14)	44.6 (43-46)	87.6 (86-90)	40.3 (39-42)	39.0 (39)	35.0 (35)
<i>P. gracilis</i> n = 26	50.9 (48-55)	54.4 (50-57)	26.3 (24-30)	12.7 (11-14)	9.4 (8-10)	38.5 (35-43)	73.5 (58-86)	35.0 (30-40)	44.8 (43-47)	41.0 (40-42)
<i>P. irinae</i> n = 59	51.3 (48-54)	55.0 (53-58)	27.2 (25-29)	13.1 (12-15)	10.4 (9-12)	38.0 (34-42)	81.5 (73-93)	37.5 (35-41)	43.2 (41-45)	40.0 (39-41)
<i>P. trimaculatus</i> n = 47	51.4 (48-57)	55.0 (52-60)	27.7 (21-32)	13.1 (12-15)	10.4 (9-12)	37.5 (32-44)	80.3 (61-99)	38.1 (34-44)	42.4 (41-44)	39.1 (38-41)
<i>S. cingulatus</i> n = 6	54.1 (52-56)	52.5 (51-54)	28.1 (27-29)	17.0 (16-19)	10.6 (10-11)	44.4 (40-48)	68.8 (64-68)	26.8 (24-30)	37.9 (37-39)	34.5 (34-35)
<i>S. respectus</i> n = 3	52.3 (52-53)	53.1 (52-53)	30.0 (29-30)	18.7 (18-20)	10.8 (10-11)	43 (42-46)	68.1 (67-69)	39.3 (38-40)	39.3 (39-40)	35.0 (35)

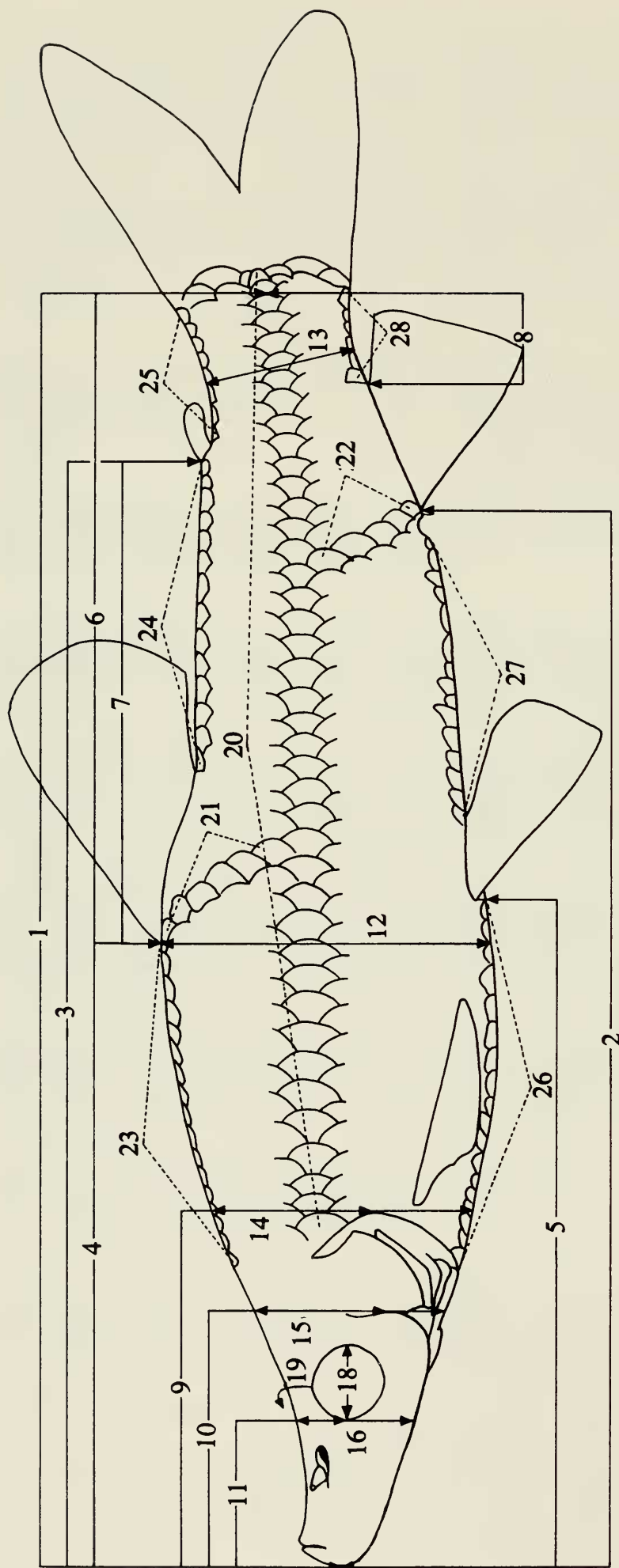


Fig. 1 Left lateral view of a hypothetical anostomine to show methods of measuring and counting. Not shown are circumpeduncular scale count and body width (measured at the pectoral fins).
 1) standard length, 2) lower jaw to anal-fin origin, 3) lower jaw to adipose-fin origin, 4) lower jaw to dorsal-fin origin, 5) lower jaw to pelvic-fin origin, 6) dorsal-fin origin to caudal-fin origin, 7) dorsal-fin origin to adipose-fin origin, 8) caudal peduncle length, 9) head length, 10) preopercle length, 11) snout length, 12) body depth, 13) caudal peduncle depth, 14) head depth, 15) preopercle depth, 16) snout depth, (17 = body width, not shown), 18) eye diameter, 19) bony interorbital, 20) lateral-line scales, 21) dorsal transverse scales, 22) ventral transverse scales, 23) predorsal scales, 24) dorsal to adipose scales, 25) adipose to caudal scales, 26) isthmus to pelvis scales, 27) pelvis to anus scales, 28) anal to caudal scales, (29 = circumpeduncular scales, not shown).

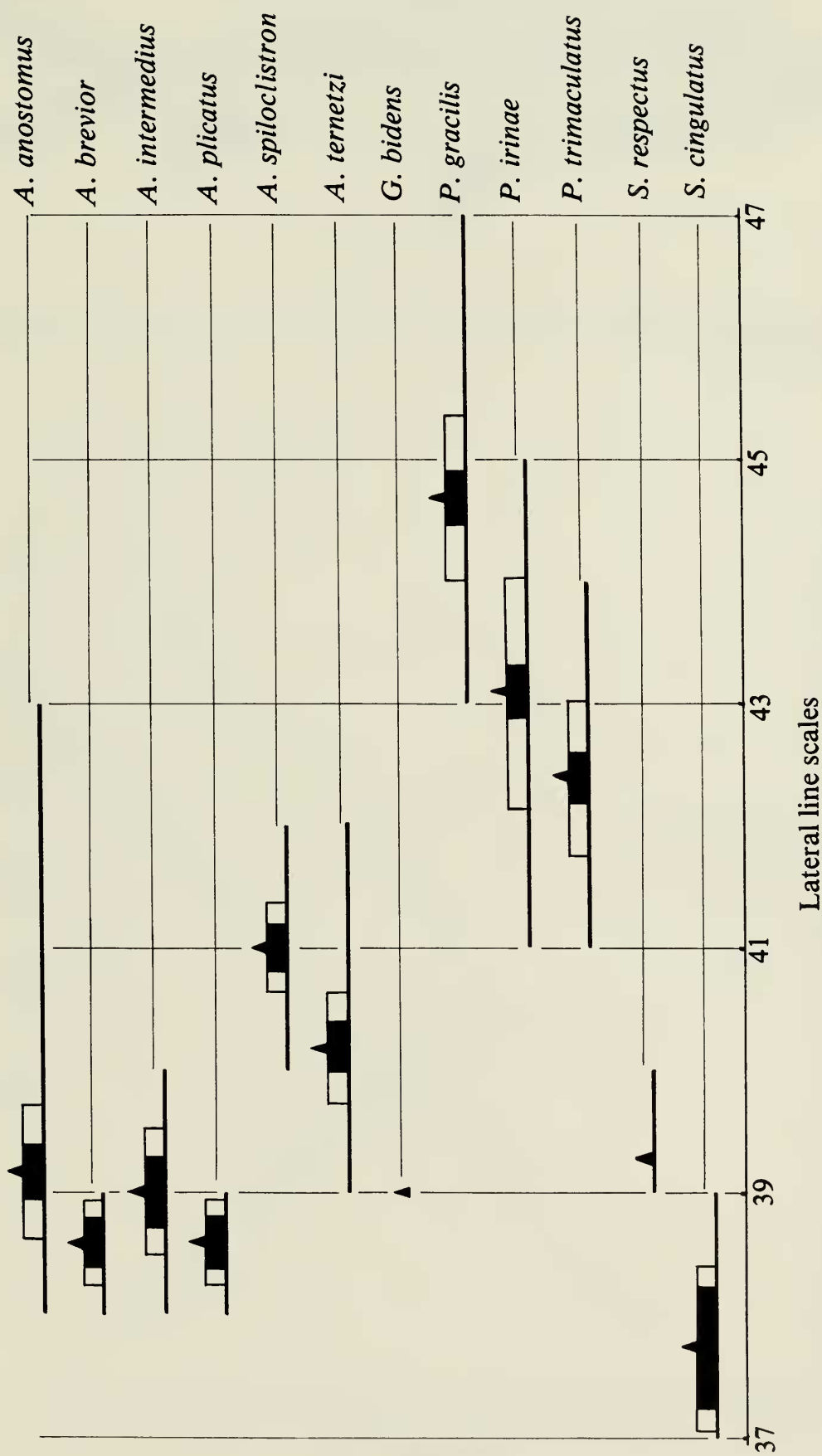


Fig. 2 Hubbs-Hubbs diagram of the lateral-line scale counts of anostomine characoids. Baseline equals range, small black triangle equals mean, black area is one standard error on either side of mean and black plus clear area represents one standard deviation on either side of mean.

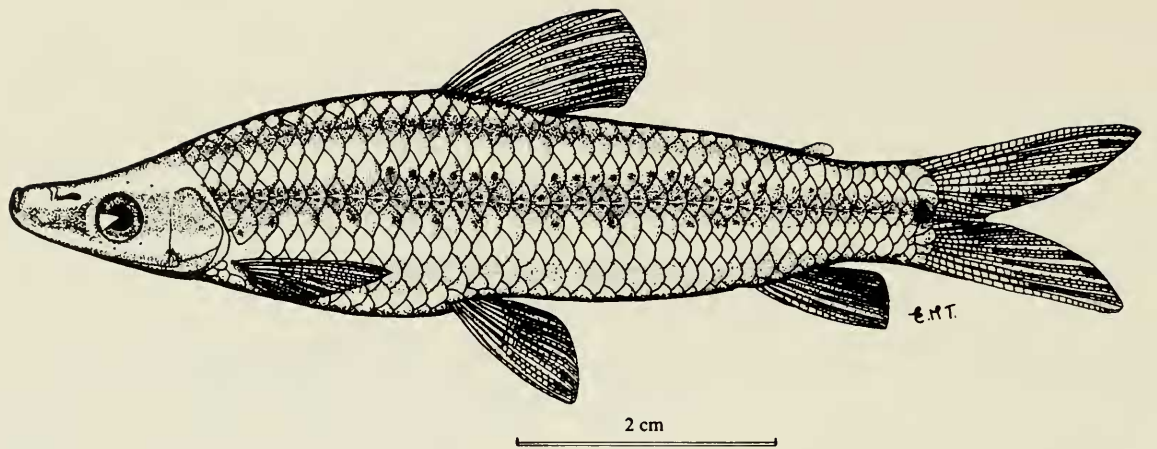


Fig. 3 Left lateral view of *Anostomus anostomus* (ZMA 106.528, 67.6 mm SL). Fins artificially figured as though spread.

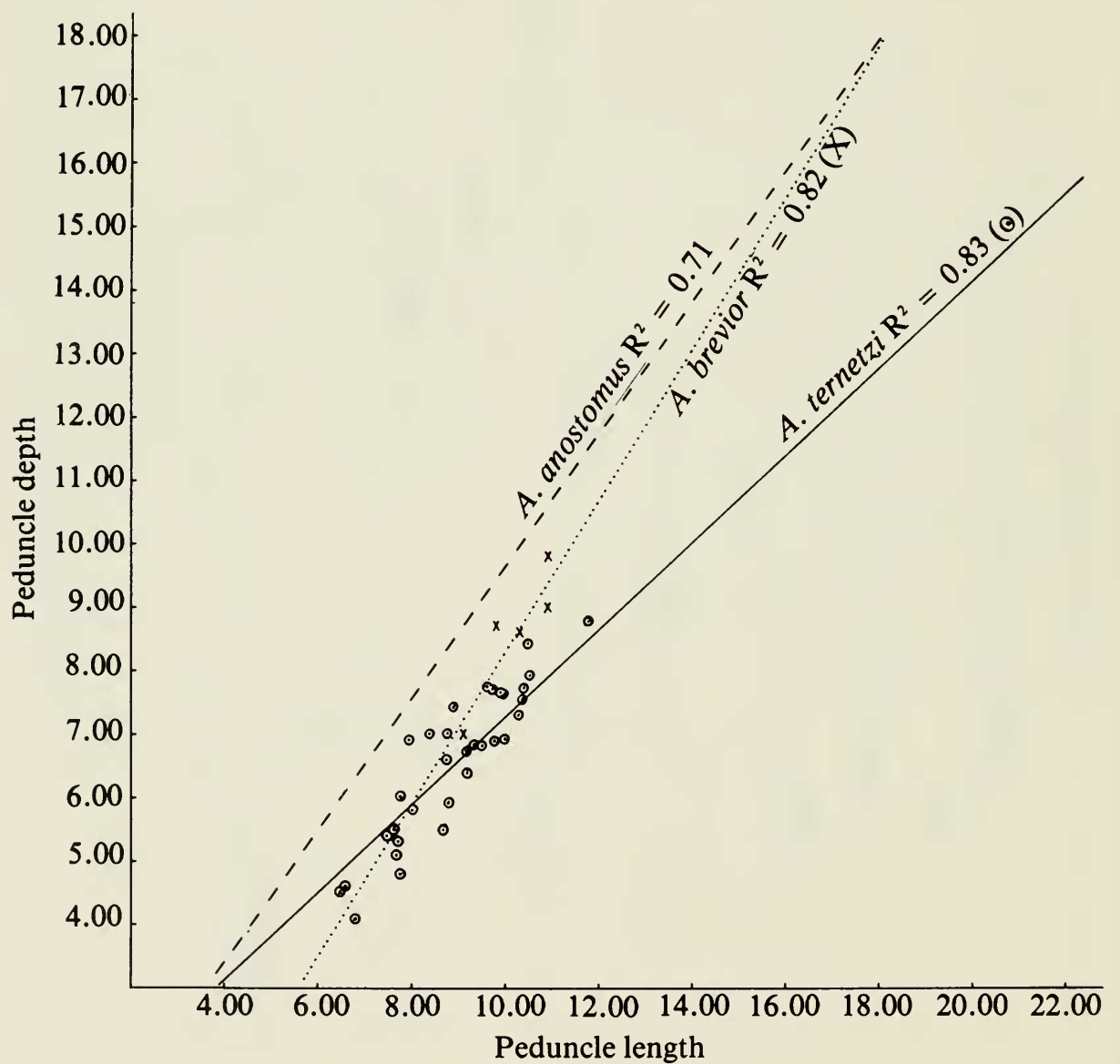


Fig. 4 Graph showing regression lines of peduncle length vs peduncle depth for *Anostomus anostomus*, *A. brevior* (points plotted), and *A. ternetzi* (points plotted).

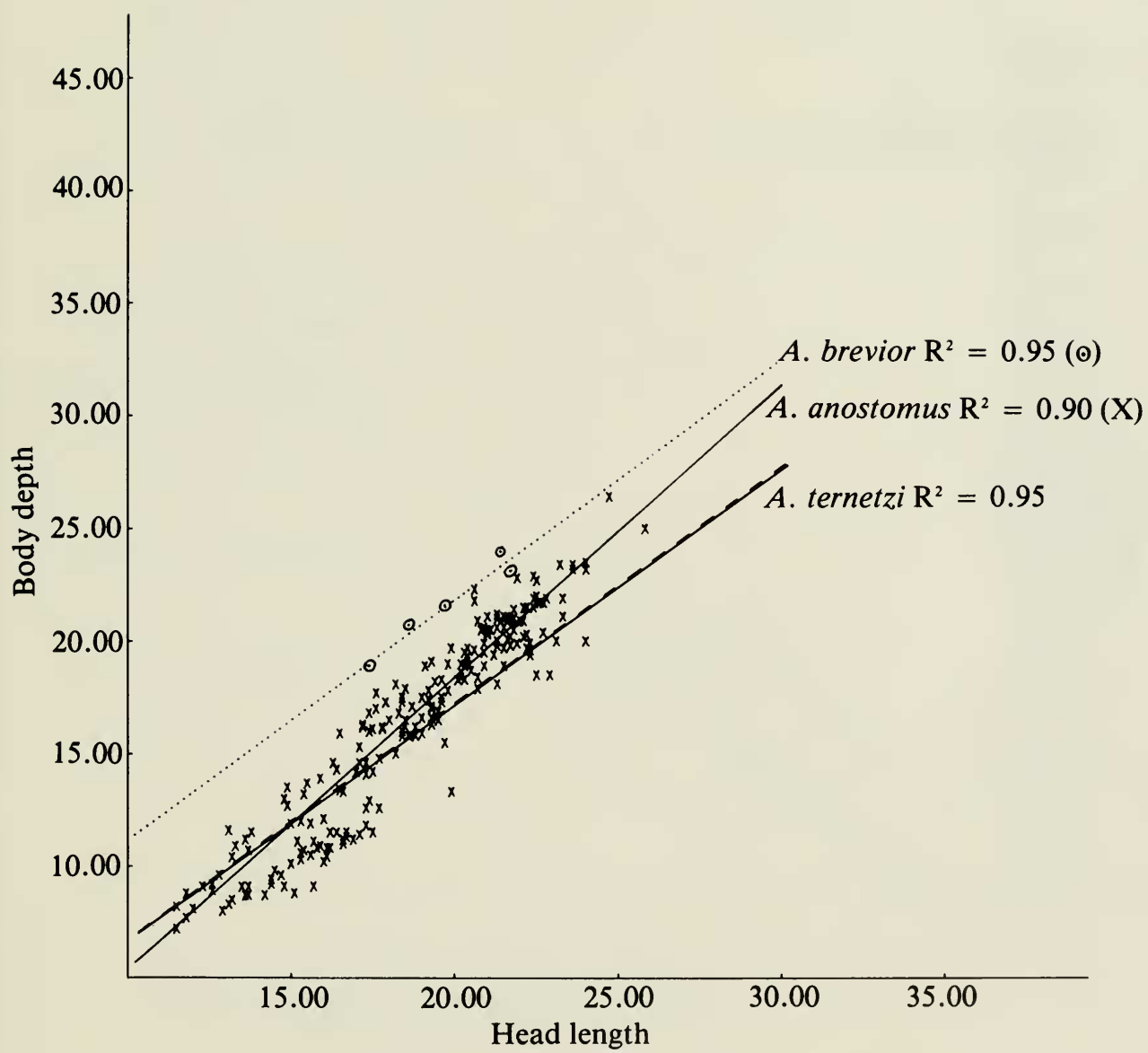


Fig. 5 Graph showing regression lines of head length vs body depth for *Anostomus anostomus* (points plotted), *A. brevior* (points plotted), and *A. ternetzi*.

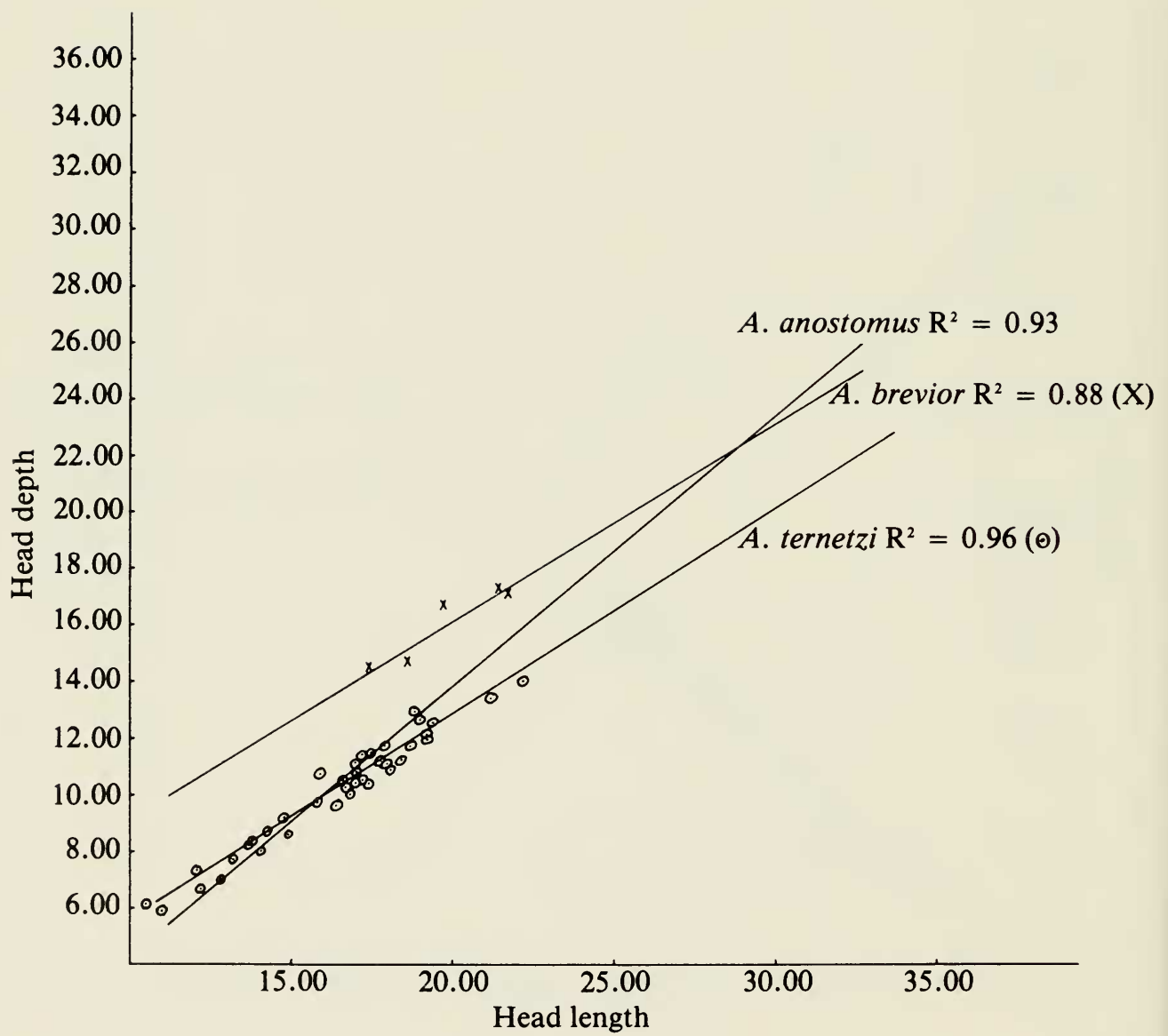


Fig. 6 Graph showing regression lines of head length vs head depth for *Anostomus anostomus*, *A. brevior* (points plotted), and *A. ternetzi* (points plotted).

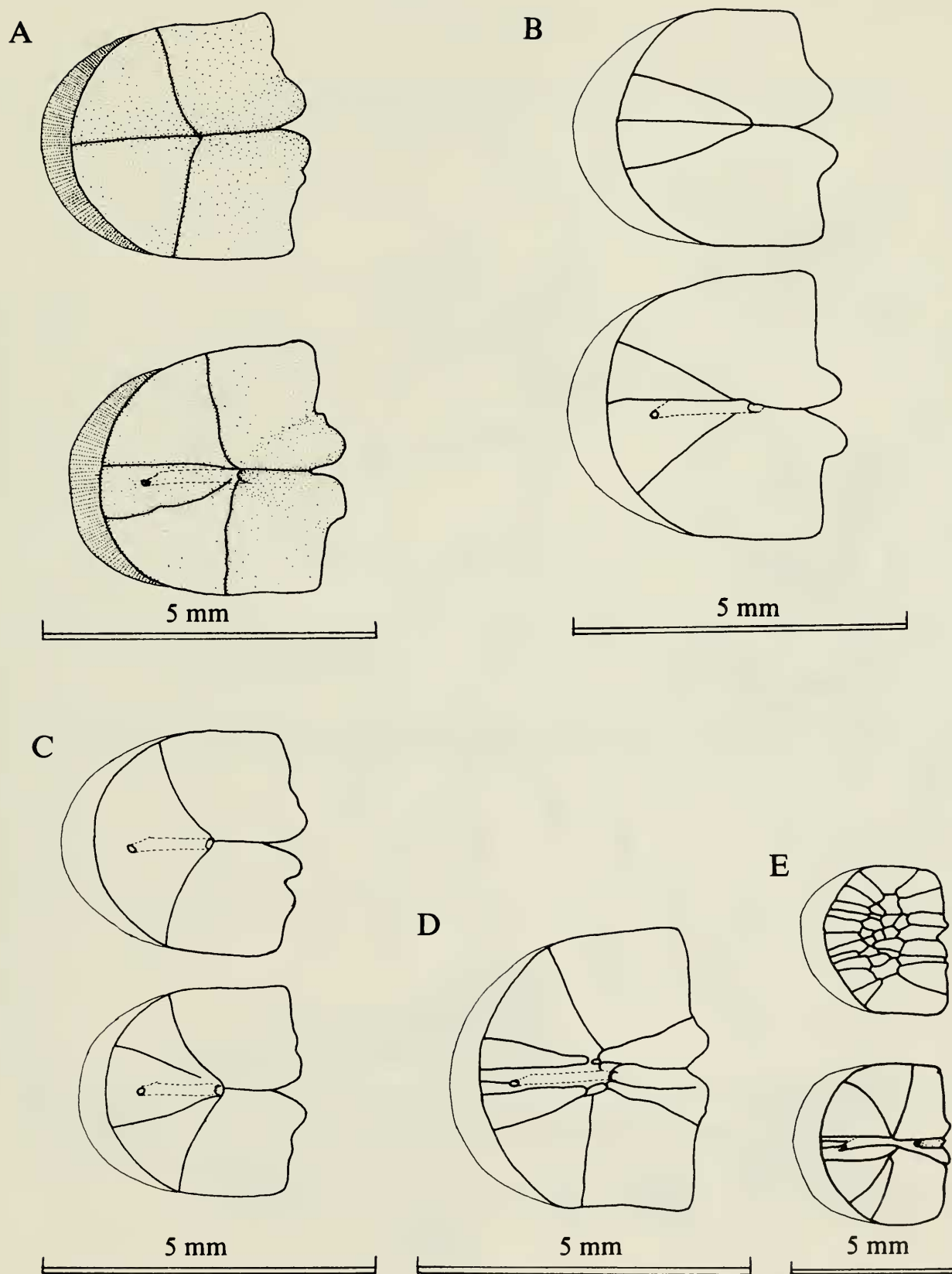


Fig. 7 Anostomine scales (taken from right side of body, below the dorsal fin origin, representing the scale row above the lateral line (upper) and the lateral line (lower)).

- A. *Anostomus anostomus*, aquarium specimen, 78.0 mm SL.
- B. *Pseudanos gracilis*, SU 16280, 91.3 mm SL.
- C. *P. irinae*, SU 16281, 66.2 mm SL.
- D. *A. plicatus*, AMNH 17602, 73.5 mm SL, lateral-line scale only.
- E. *Synaptolaemus cingulatus*, MBUVC V-4252, 71.2 mm SL.

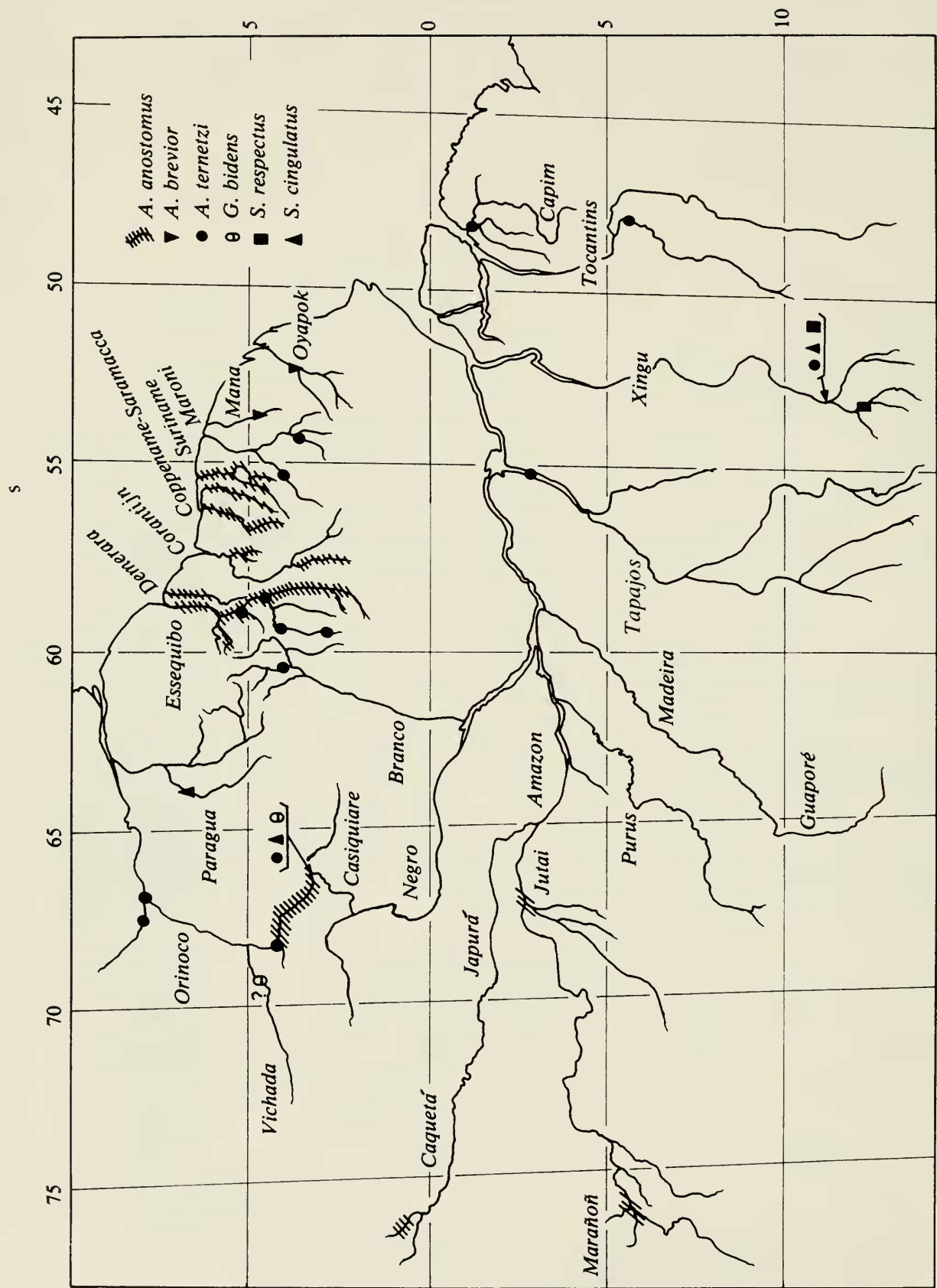


Fig. 8 Distribution map of the striped *Anostomus* species (*A. anostomus*, *A. brevior* and *A. ternetzi*) and the three monotypic anostomine genera (*Gnathodolus bidens*, *Sartor respectus* and *Synaptolaemus cingulatus*).

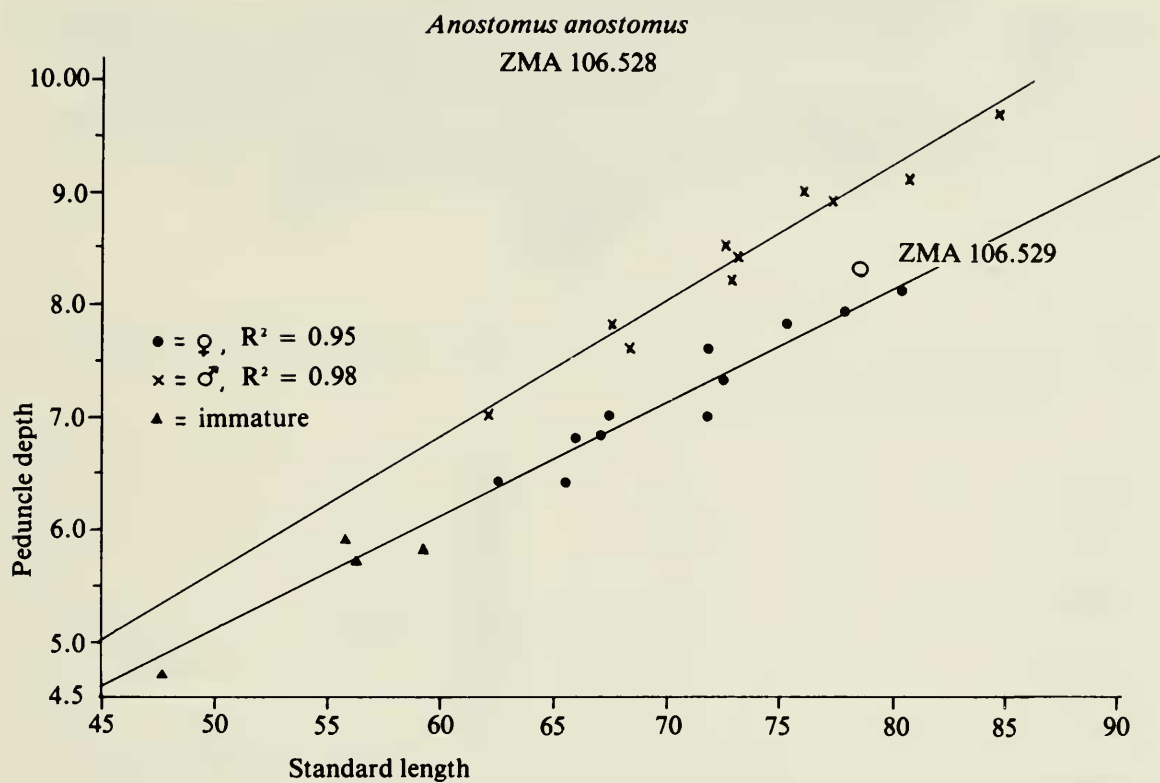


Fig. 9 Graph of standard length vs peduncle depth for *Anostomus anostomus* (ZMA 106.528, 25, and ZMA 106.529, 1). R^2 calculated for males and for females plus juveniles.

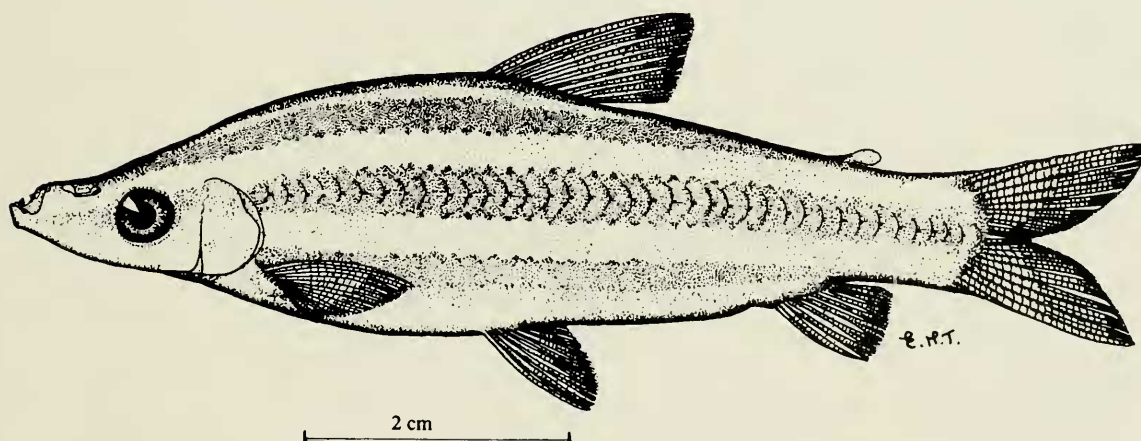


Fig. 10 Left lateral view of *Anostomus brevior* (MNHN 01-407, 72.6 mm SL, paratype). Fins artificially figured as though spread, only lateral line scales shown.

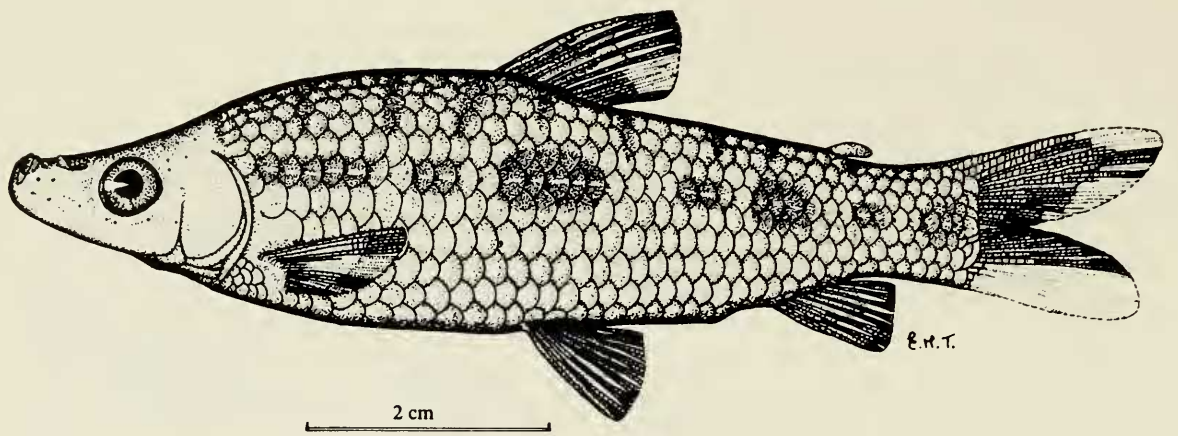


Fig. 11 Left lateral view of *Anostomus intermedius* sp. nov. (SMF13618, 77.7 mm SL, holotype). Fins artificially figured as though spread.

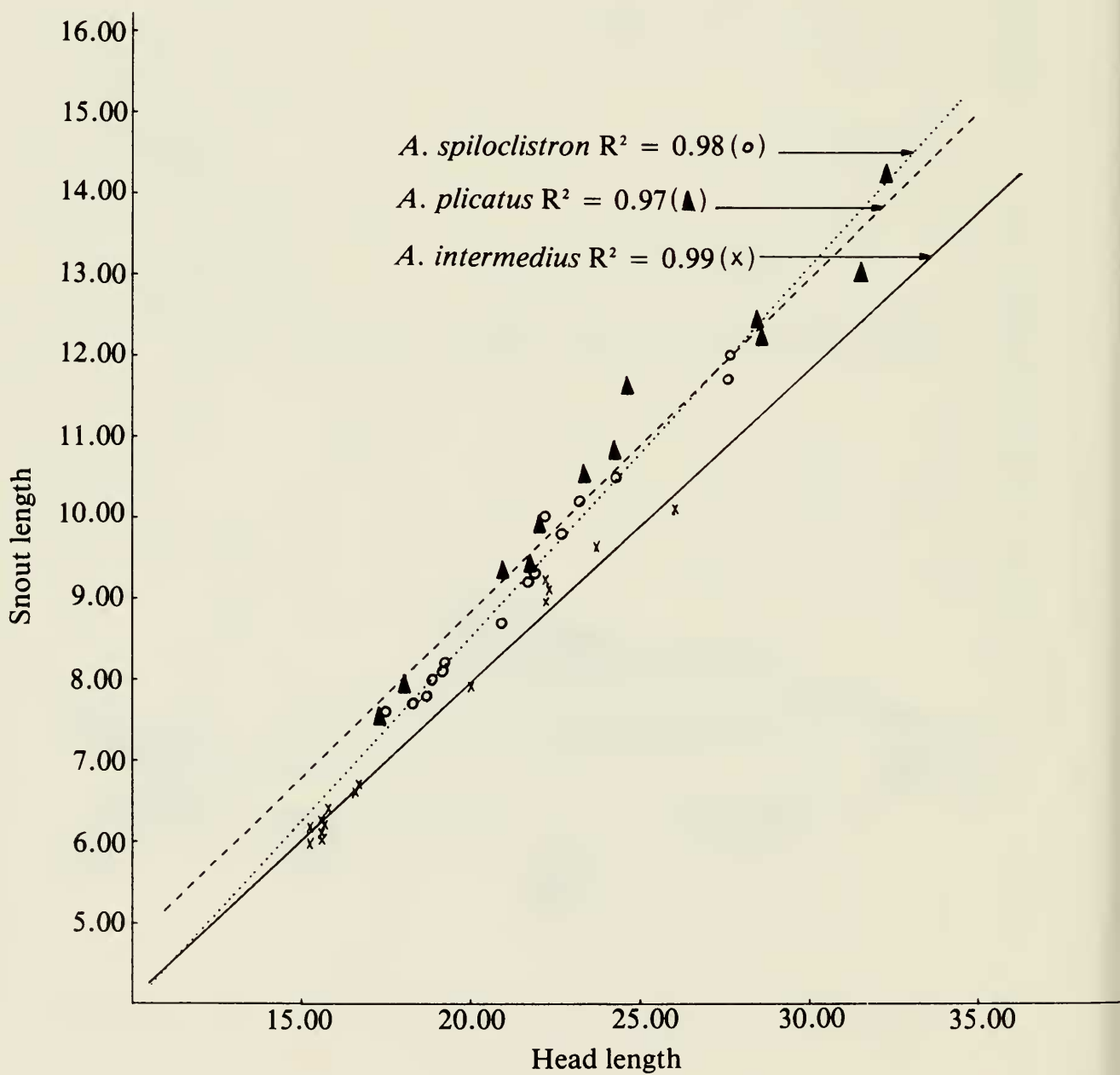


Fig. 12 Graph showing regression lines and points of head length vs snout length for *Anostomus intermedius*, *A. plicatus*, and *A. spiloclistron*.

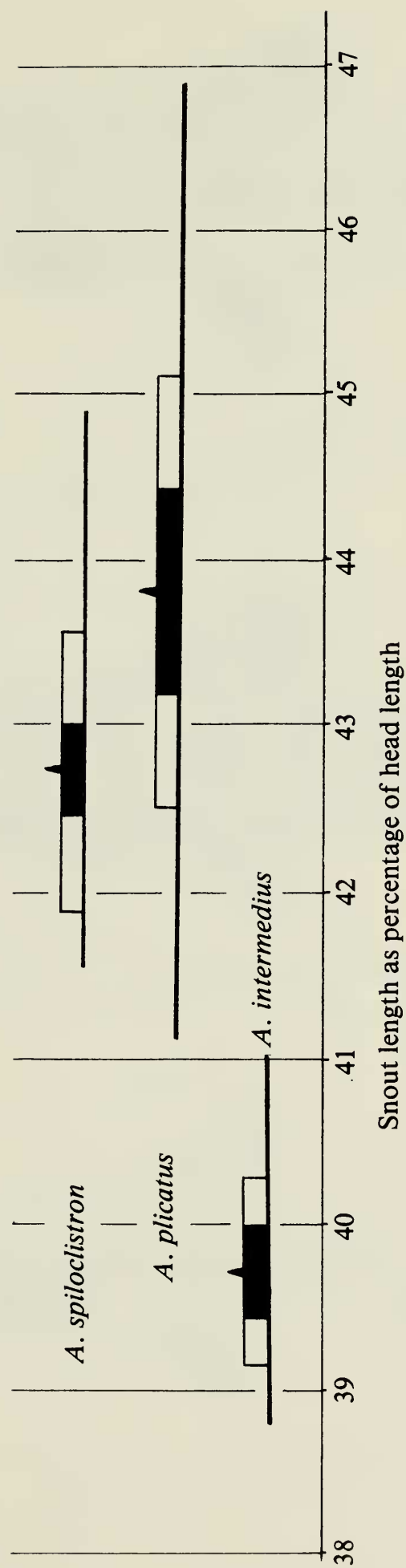


Fig. 13 Hubbs-Hubbs diagram of snout length as percentage of head length for *Anostomus intermedius*, *A. plicatus* and *A. spiloclistron*.

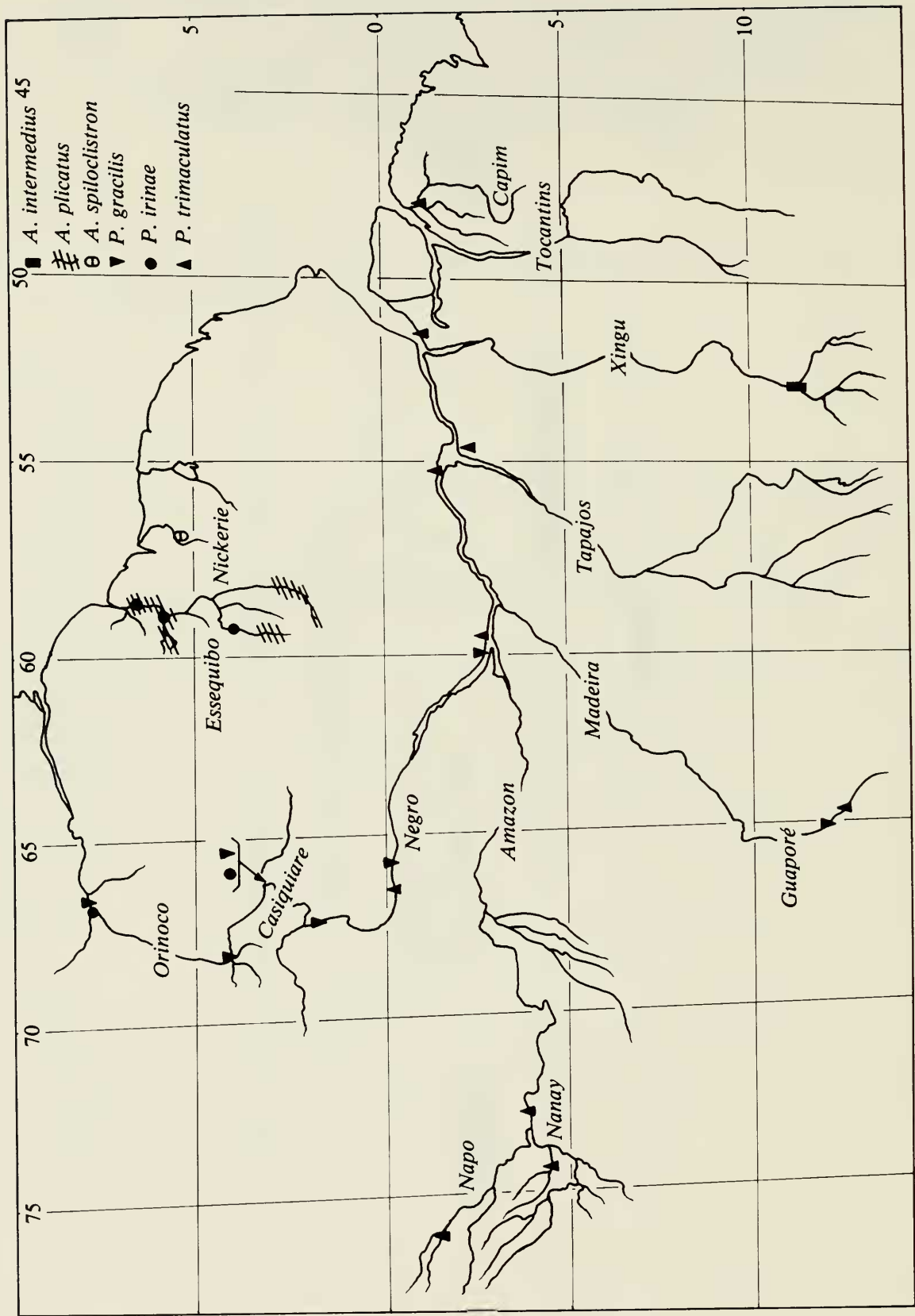


Fig. 14 Distribution map for *Anostomus intermedius*, *A. plicatus*, *A. spiloclistron*, *Pseudanostomus gracilis*, *P. irinae*, and *P. trimaculatus*.

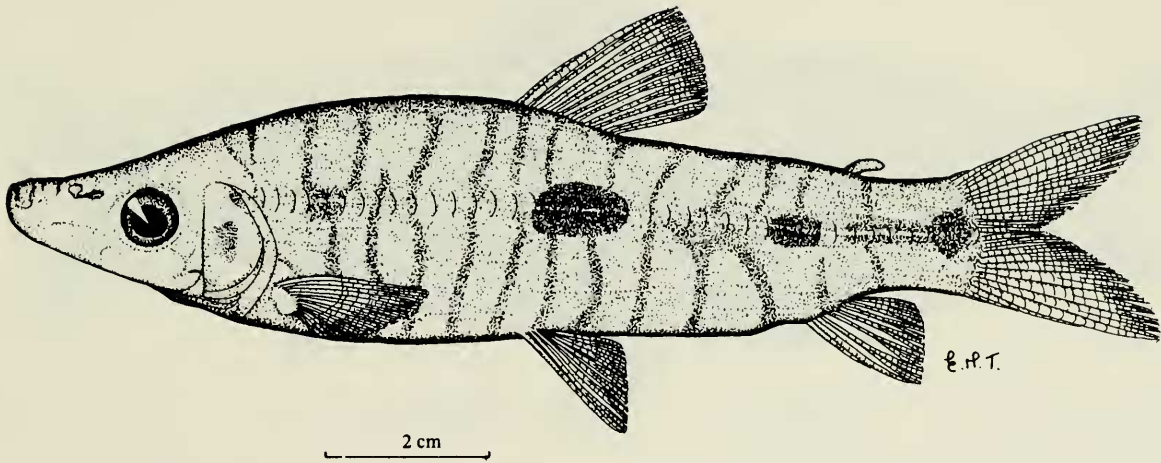


Fig. 15 Left lateral view of *Anostomus plicatus* (composite). Fins artificially figured as though spread, only lateral-line scales shown.

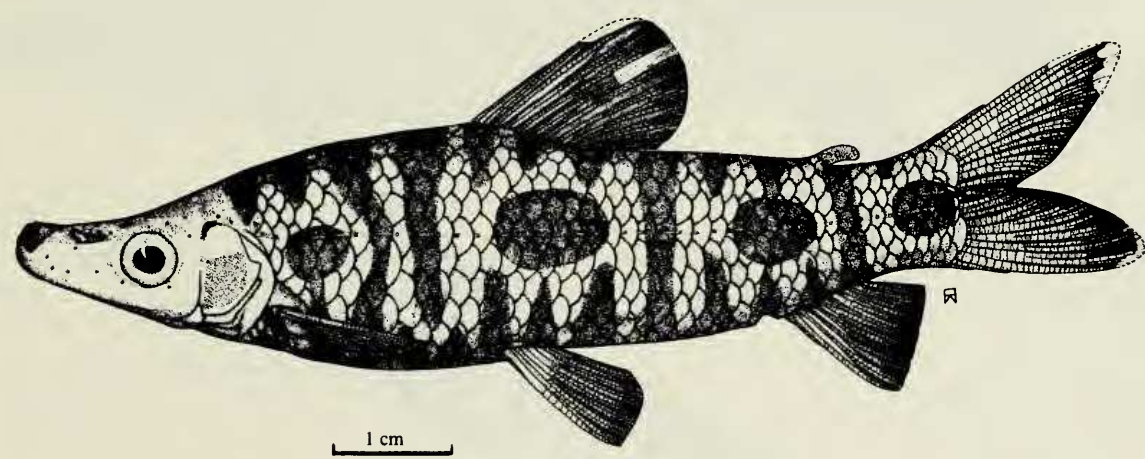


Fig. 16 Left lateral view of *Anostomus spiloclistron* (ZMA 112.685, 77.2 mm SL, holotype). Fins artificially figured as though spread (from Winterbottom, 1974a).

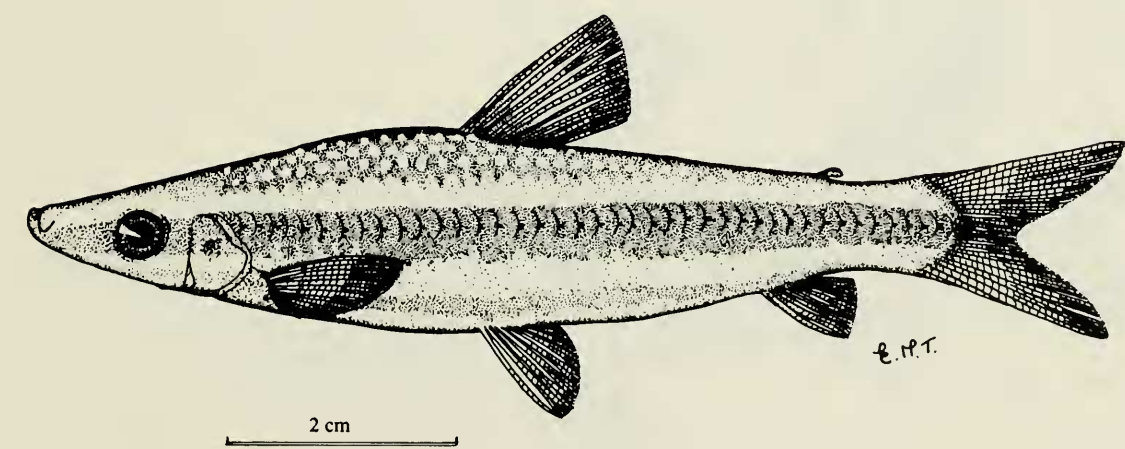


Fig. 17 Left lateral view of *Anostomus ternetzi* (MZUSP 9990, 80.0 mm SL). Fins artificially figured as though spread, only lateral-line scales shown.

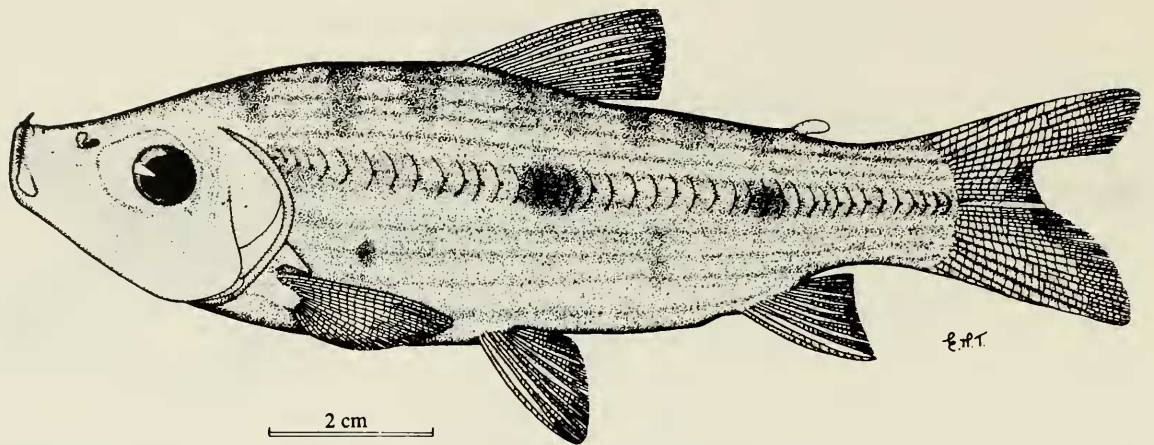


Fig. 18 Left lateral view of *Gnathodolus bidens* (CAS 20087, 108.8 mm SL, holotype). Fins artificially figured as though spread, only lateral-line scales shown.

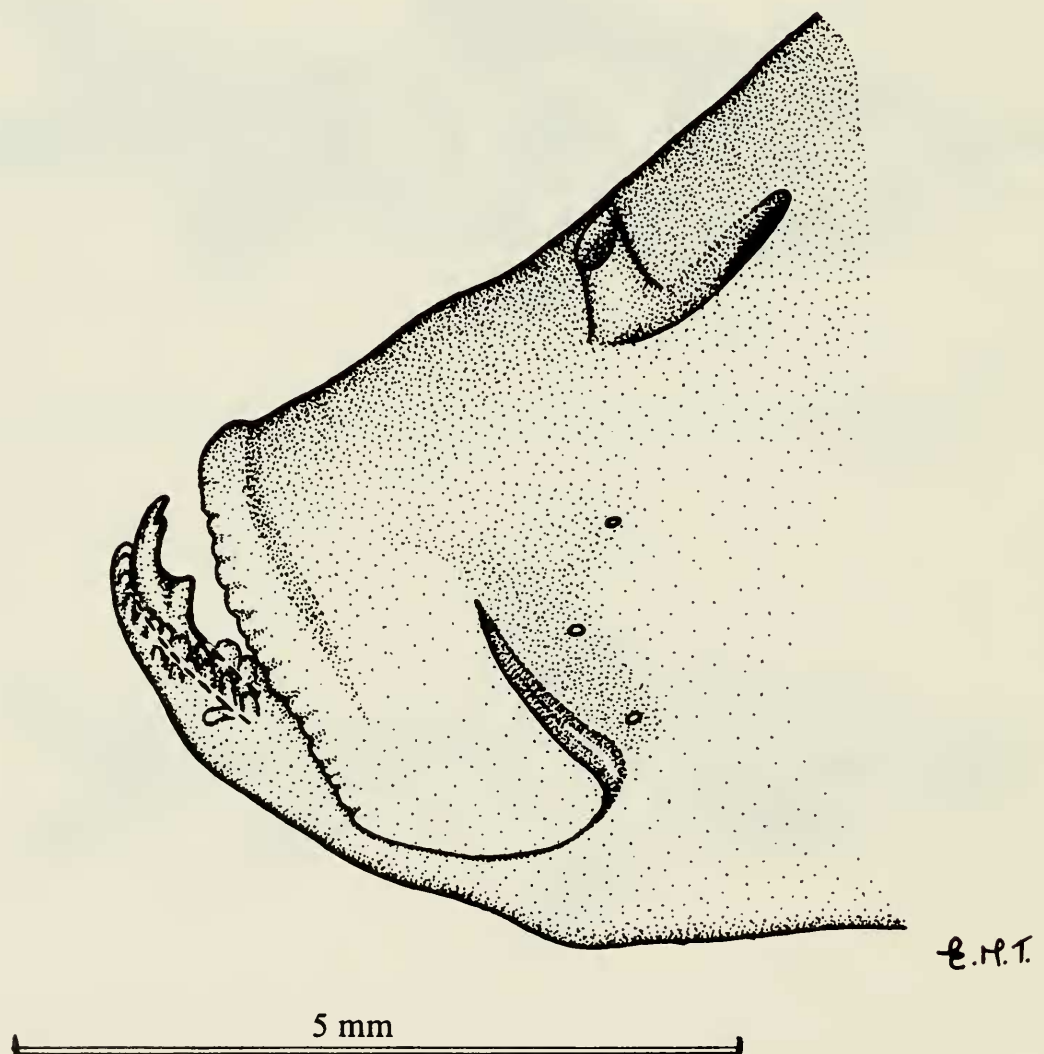


Fig. 19 *Gnathodolus* sp. (BM(NH) 1972-12-5:5, 51.5 mm SL). Left lateral view of snout to show lower jaw tooth and papillae of the lower lip.

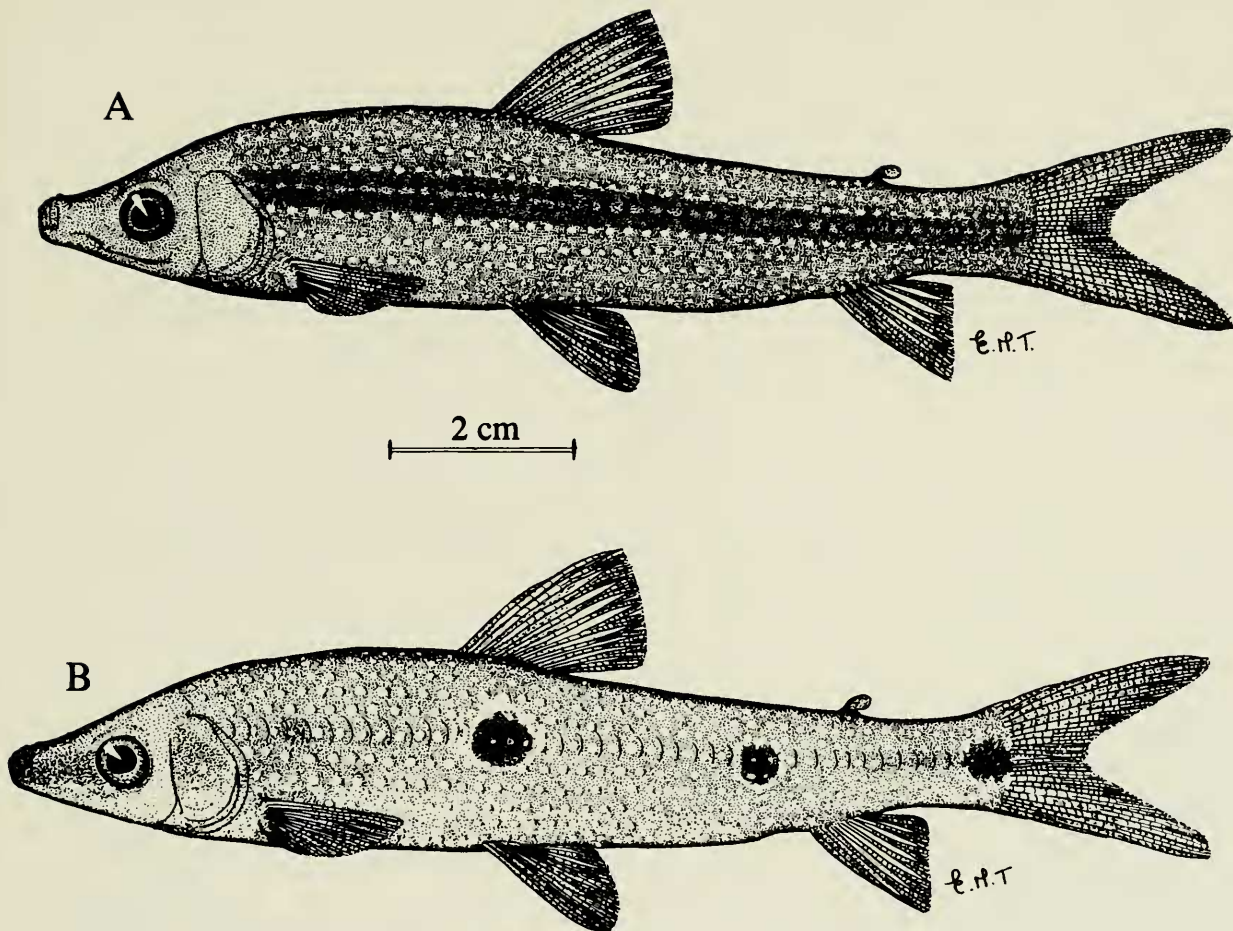


Fig. 20 Left lateral view of *Pseudanos gracilis* (composite). Fins artificially figured as though spread, only lateral-line scales shown.
 A The striped form.
 B The spotted form.

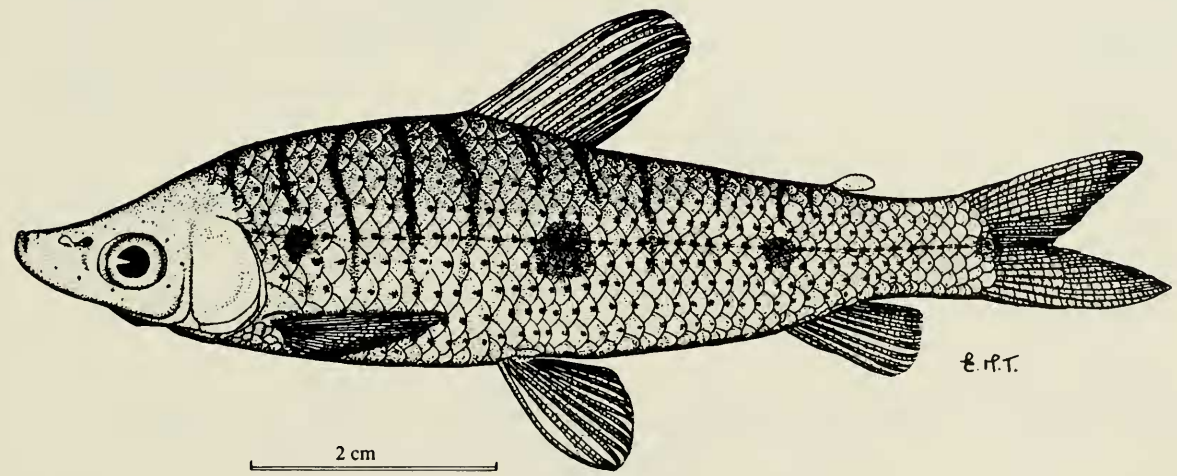


Fig. 21 Left lateral view of *Pseudanos irinae* sp. nov. (CAS 20097, 71.8 mm SL, paratype). Fins artificially figured as though spread.

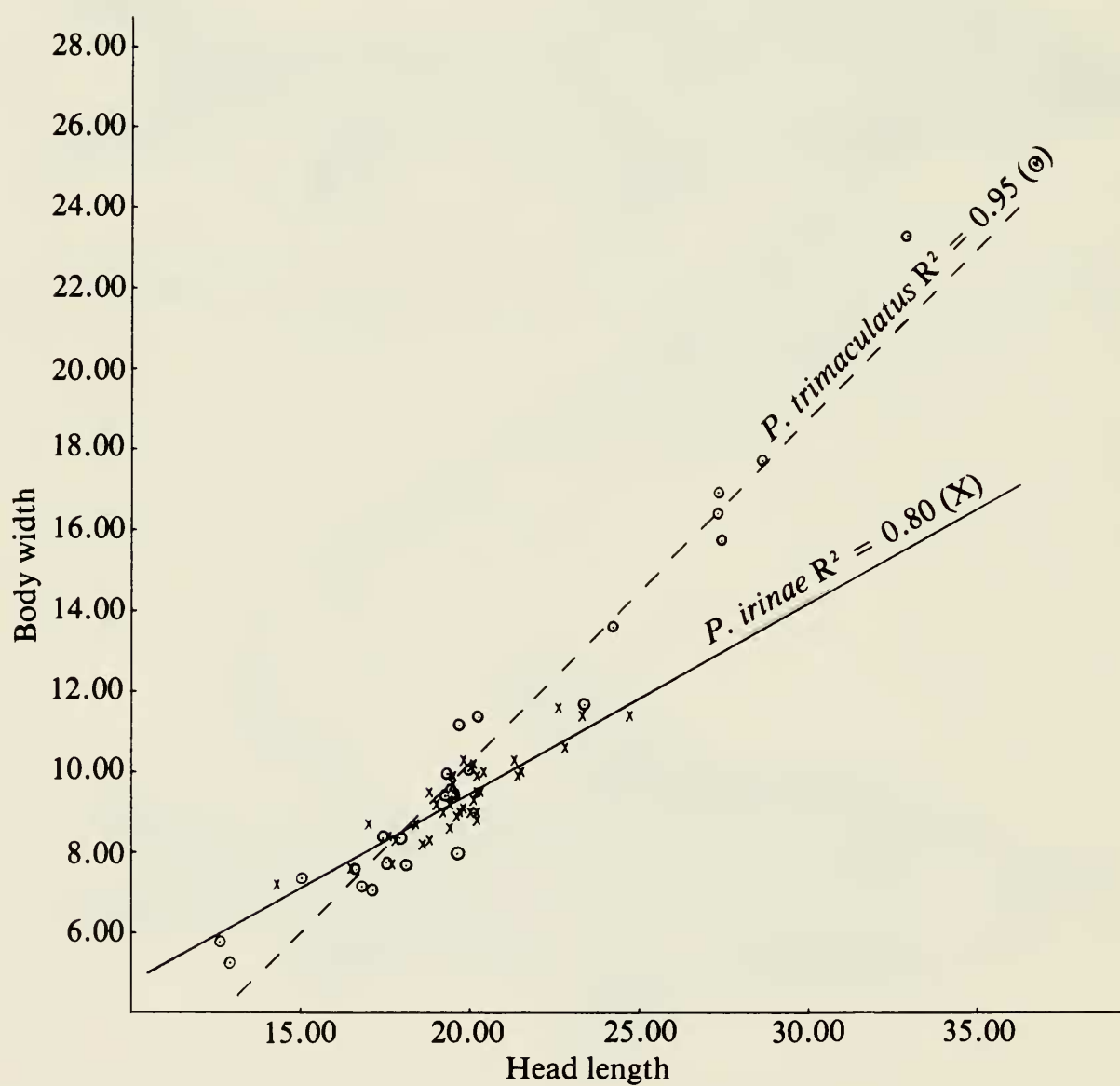


Fig. 22 Graph showing regression lines and points of head length vs body width for *Pseudanos irinae* and *P. trimaculatus*.

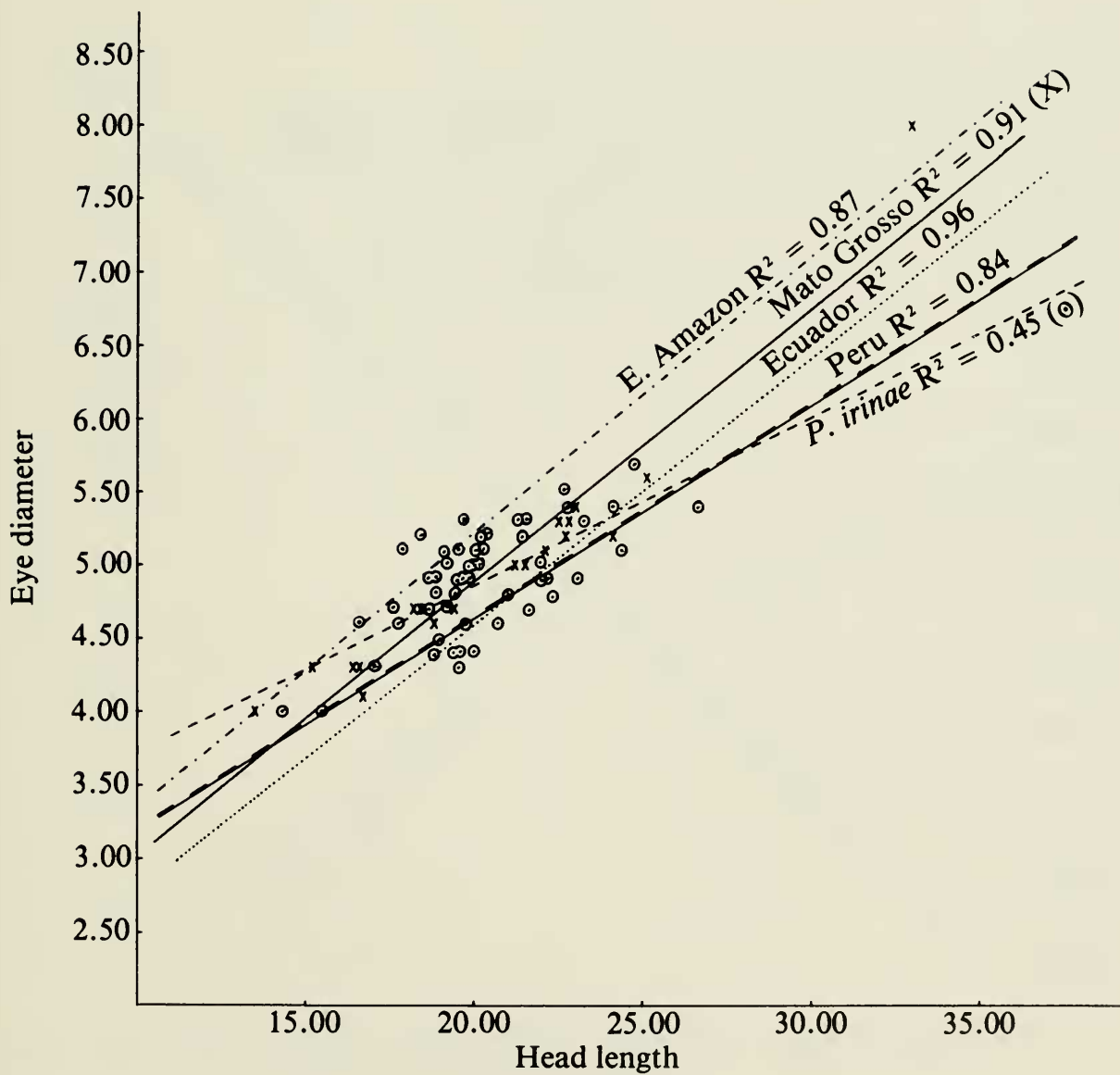


Fig. 23 Graph showing regression lines of head length vs eye diameter for *Pseudanos irinae* (points plotted) and the four populations of *P. trimaculatus* (Eastern Amazon, Ecuador, Mato Grosso—points plotted—and Peru).

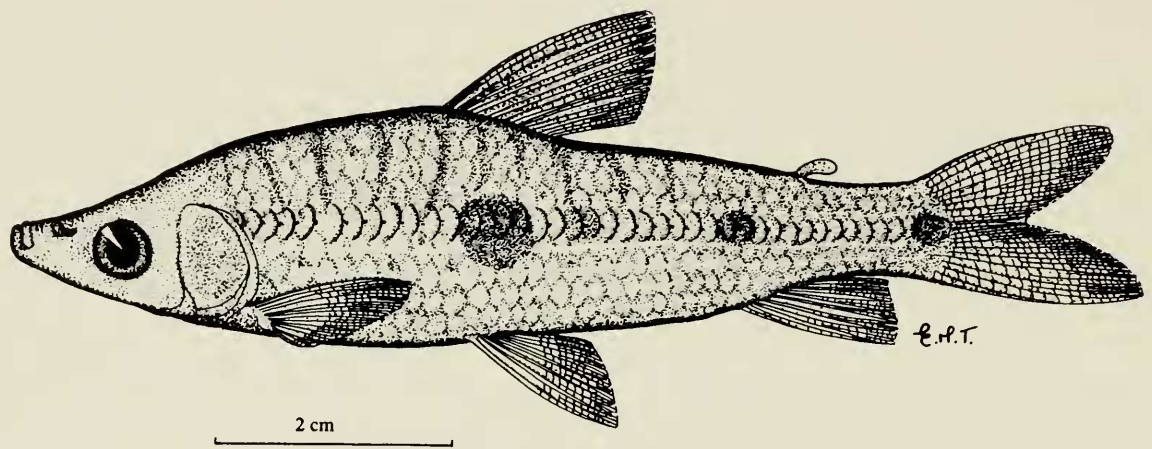


Fig. 24 Left lateral view of *Pseudanos trimaculatus* (composite). Fins artificially figured as though spread, only lateral-line scales shown.

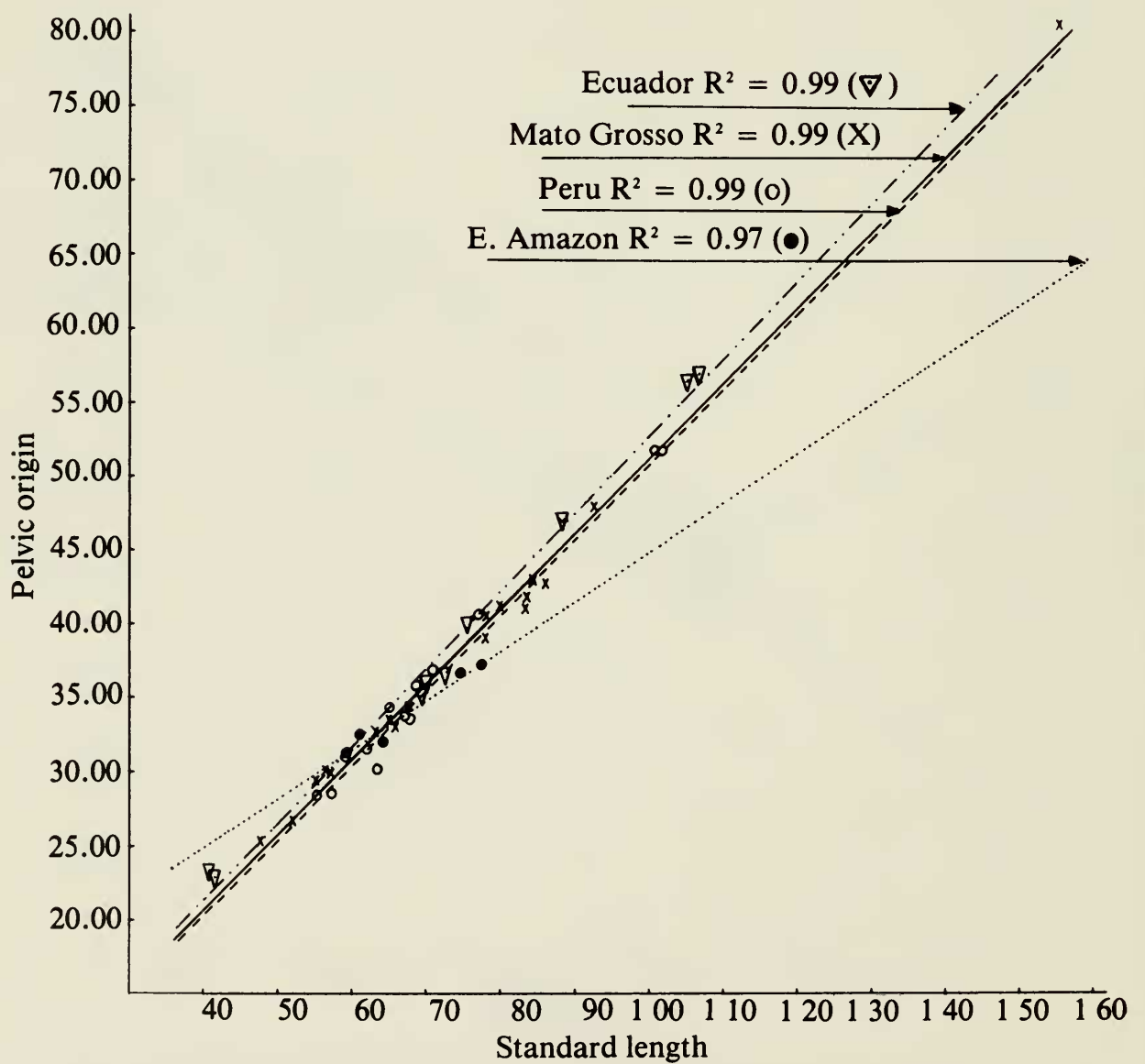


Fig. 25 Graph showing regression lines and points of standard length vs lower jaw to pelvic origin for *Pseudanos trimaculatus* populations from Eastern Amazon, Ecuador, Mato Grosso and Peru.

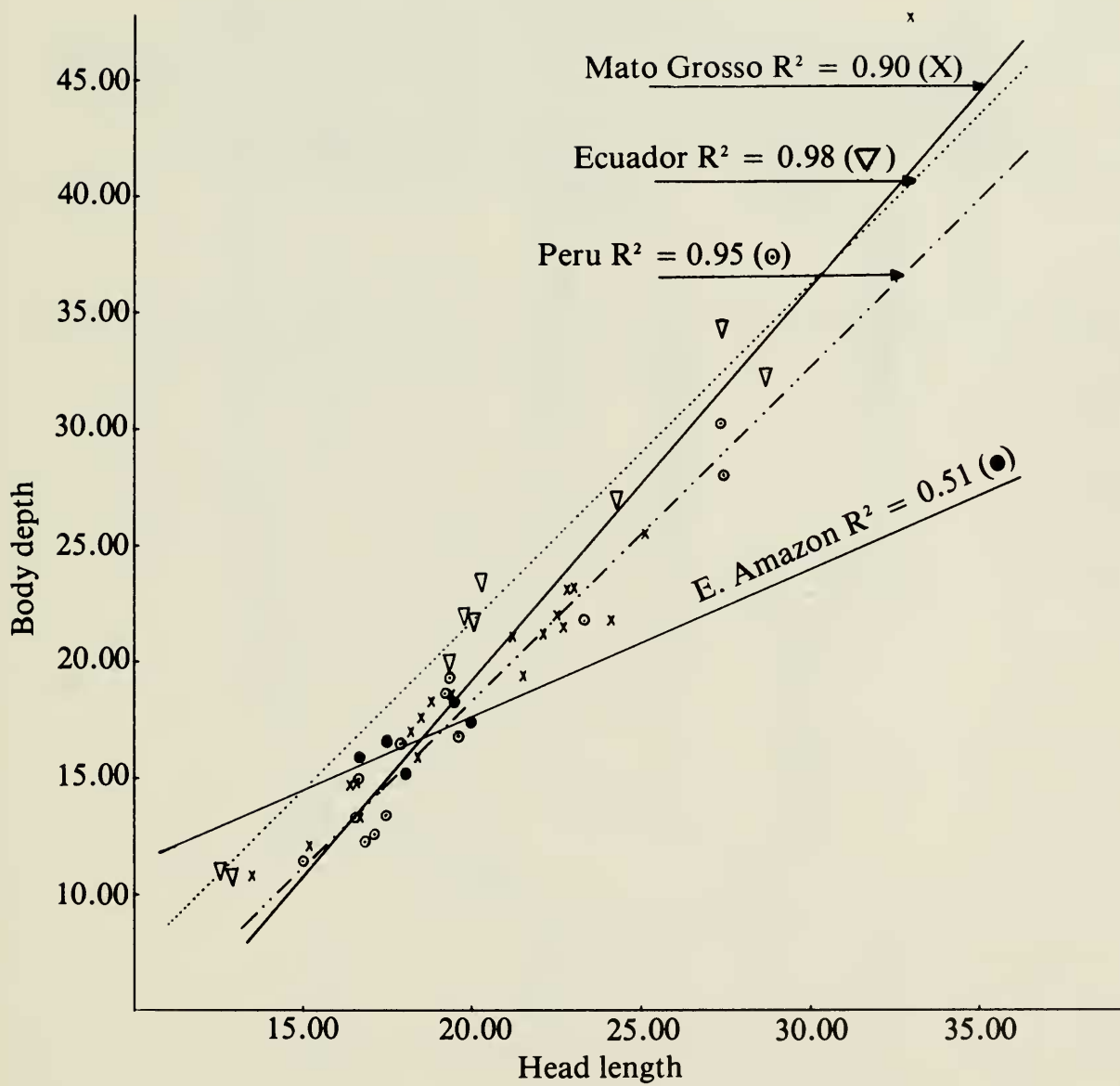


Fig. 26 Graph showing regression lines and points of head length vs body depth for *Pseudanos trimaculatus* populations from Eastern Amazon, Ecuador, Mato Grosso and Peru.

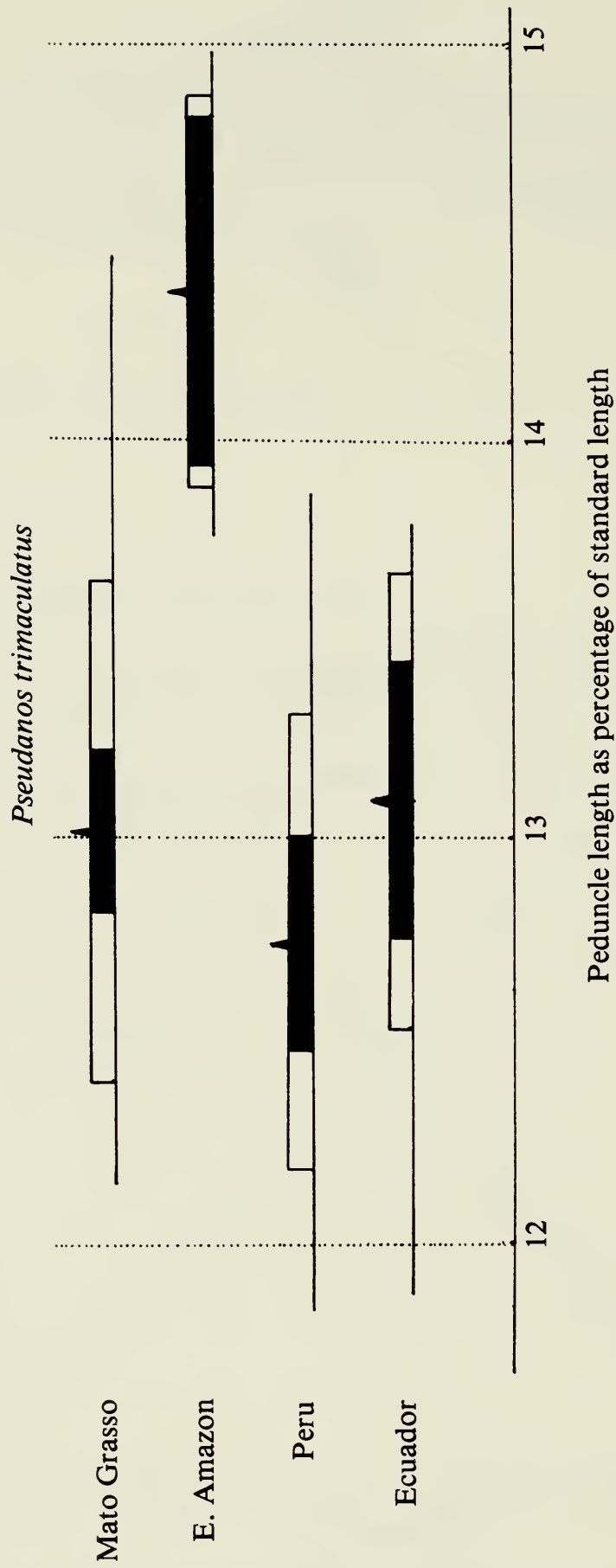


Fig. 27 Hubbs-Hubbs diagram of caudal peduncle length as a percentage of standard length for *Pseudanos trimaculatus* populations from Eastern Amazon, Ecuador, Mato Grosso, and Peru.

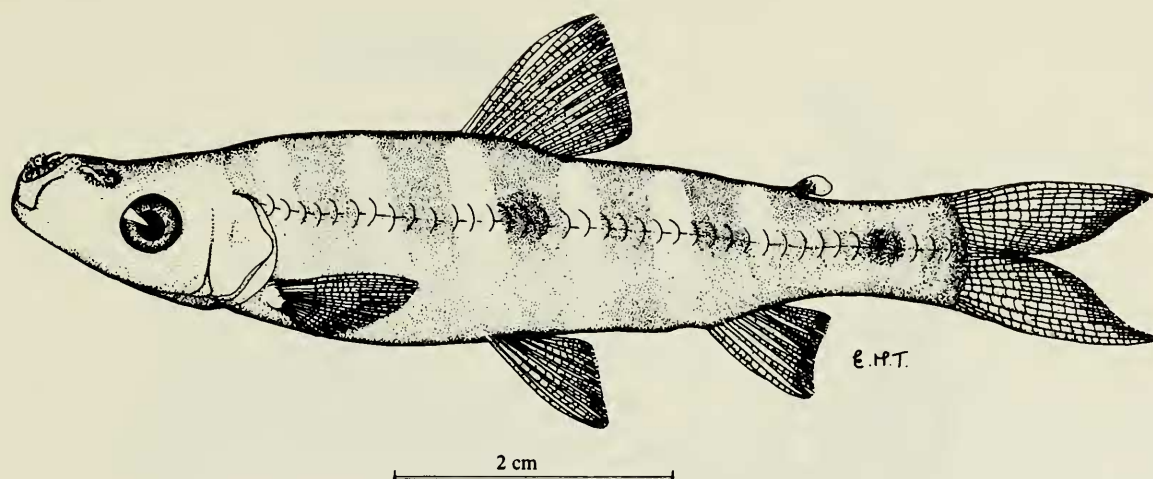


Fig. 28 Left lateral view of *Sartor respectus* (composite). Fins artificially figured as though spread, only lateral-line scales shown.

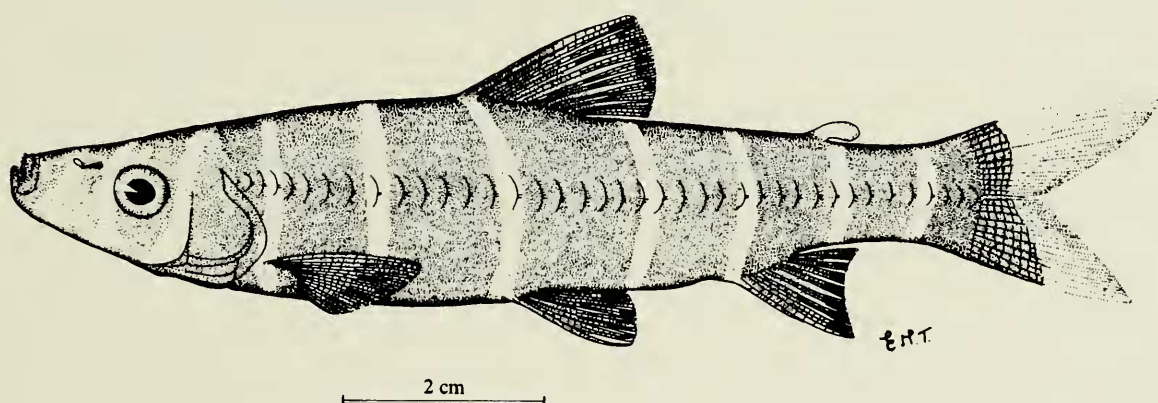


Fig. 29 Left lateral view of *Synaptolaemus cingulatus* (MBUCV V-4252, 90.0 mm SL). Fin artificially figured as though spread, only lateral-line scales shown.

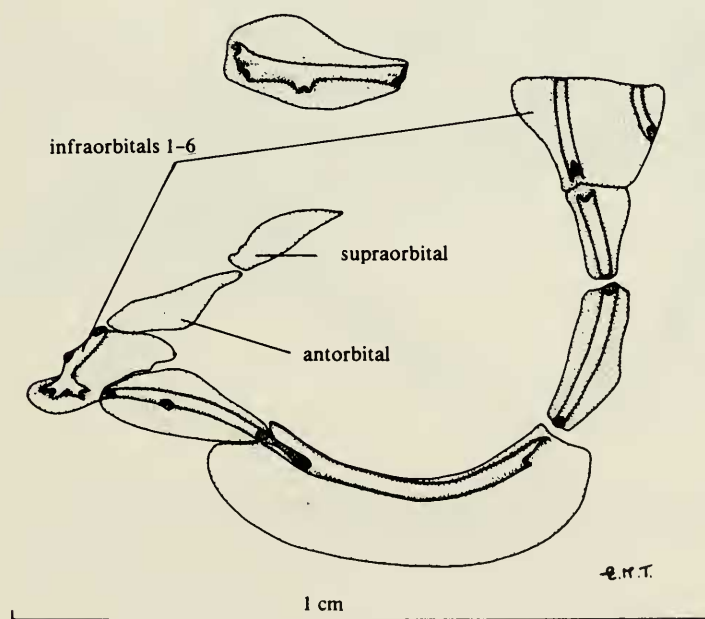


Fig. 30 *Pseudanos trimaculatus*, RUSI 5521, 52.1 mm SL. Left lateral view of the infraorbitals, antorbital and supraorbital. Inset above: dorsal view of left nasal bone from 86.0 mm SL specimen from the same collection.

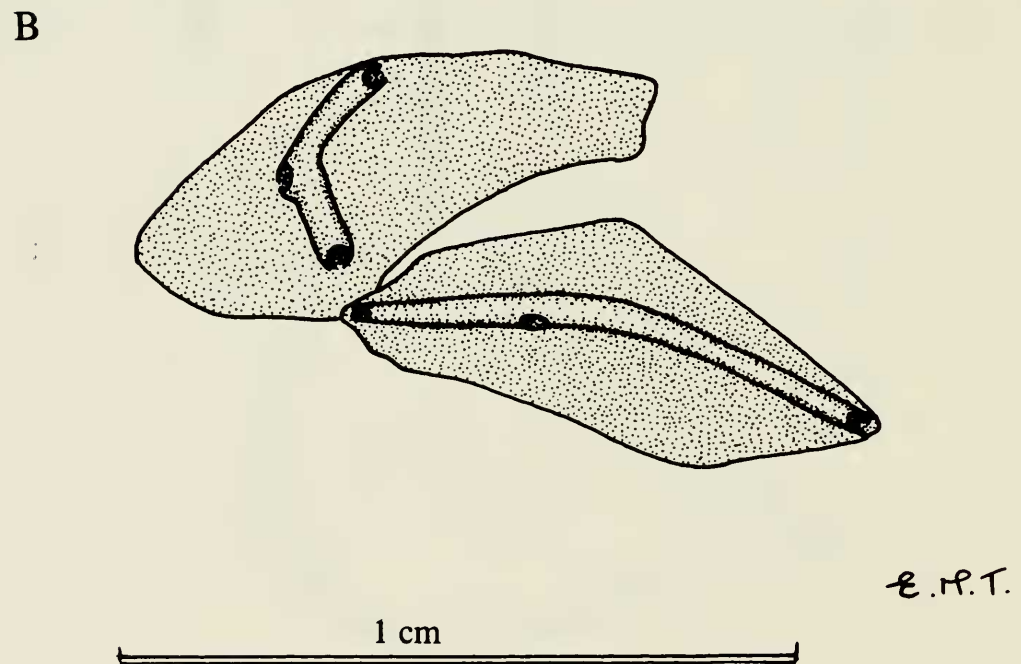
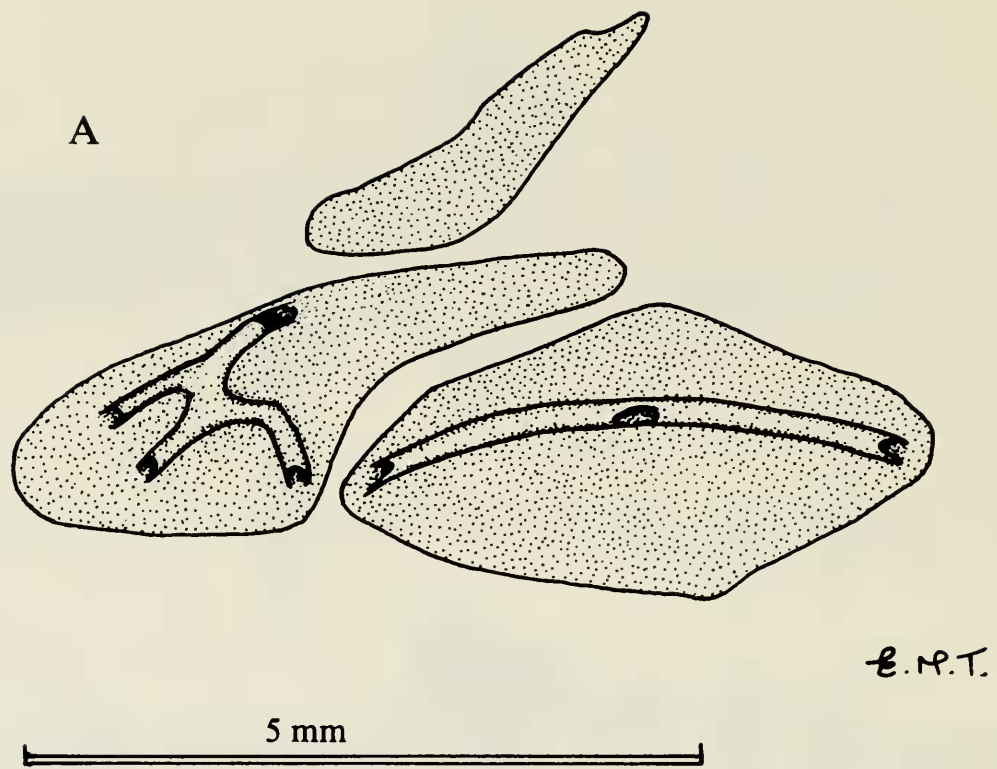


Fig. 31 A *Anostomus spiloclistron*. Left lateral view of antorbital and infraorbitals 1 and 2.
 B *Pseudanos gracilis*. Left lateral view of infraorbitals 1 and 2.

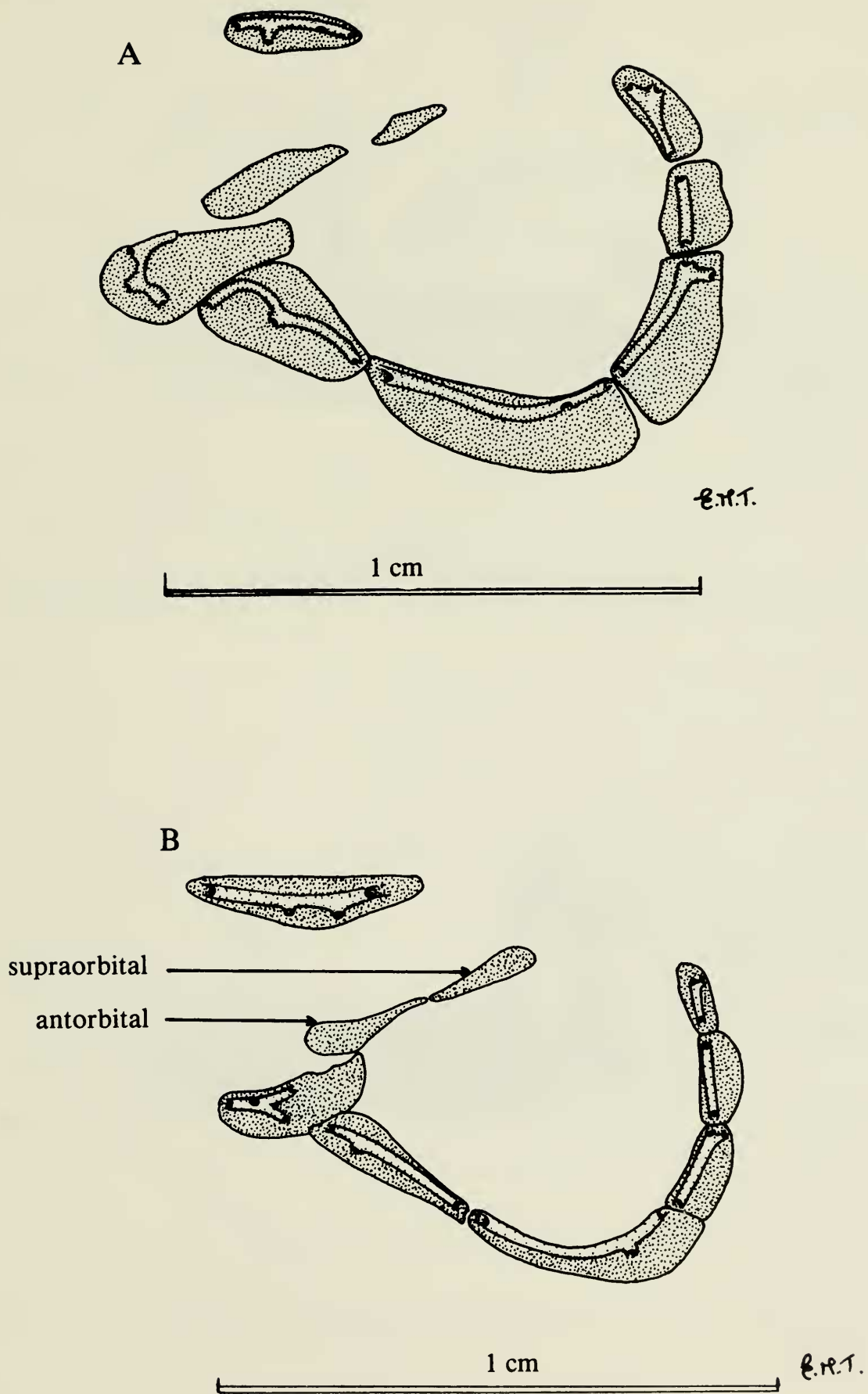


Fig. 32 A *Synaptolaemus cingulatus*. Left lateral view of infraorbital, antorbital, and supraorbital bones, with a dorsal view of the left nasal bone above.
 B *Gnathodolus* sp. Left lateral view of infraorbital, antorbital and supraorbital bones, with a dorsal view of left nasal bone above (both from mirror images of right side).

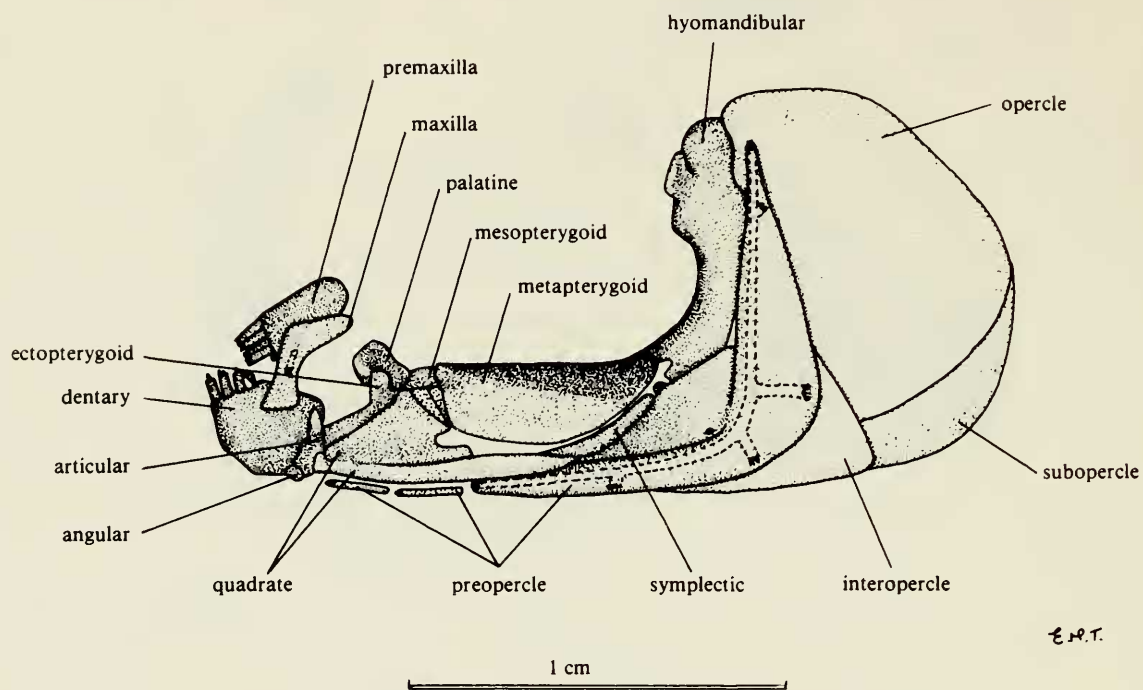


Fig. 33 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Left lateral view of suspensorium and jaws.

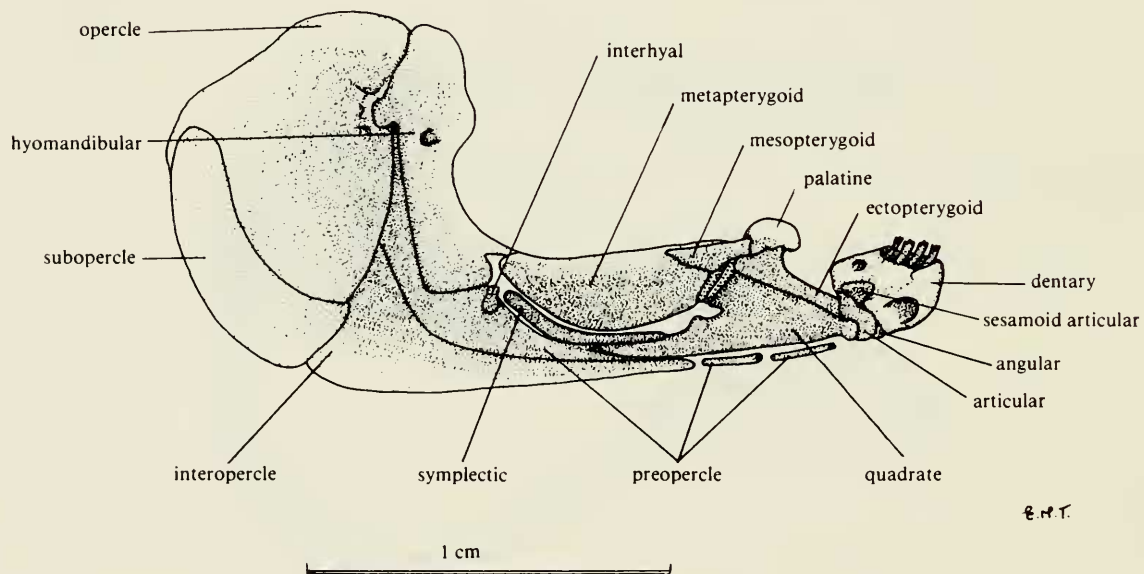


Fig. 34 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Medial view of left suspensorium and lower jaw.

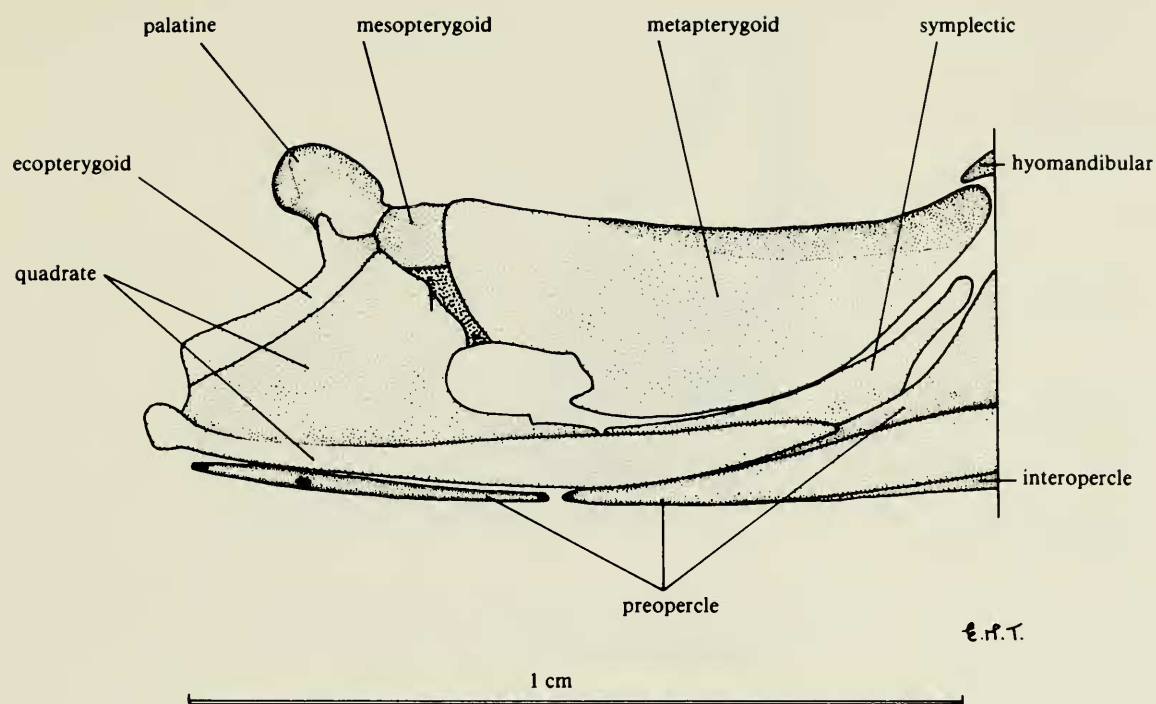


Fig. 35 *Pseudanos gracilis*. Left lateral view of anterior portion of suspensorium.

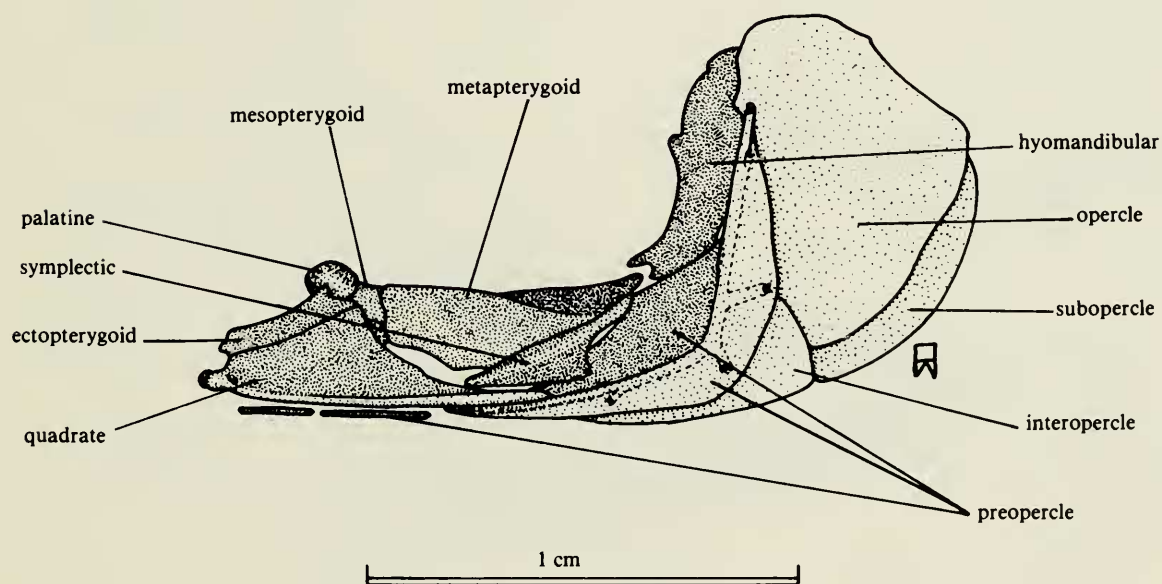


Fig. 36 *Anostomus plicatus*. Left lateral view of suspensorium.



1 mm

Fig. 37 *Anostomus plicatus*. Medial view of left premaxilla.

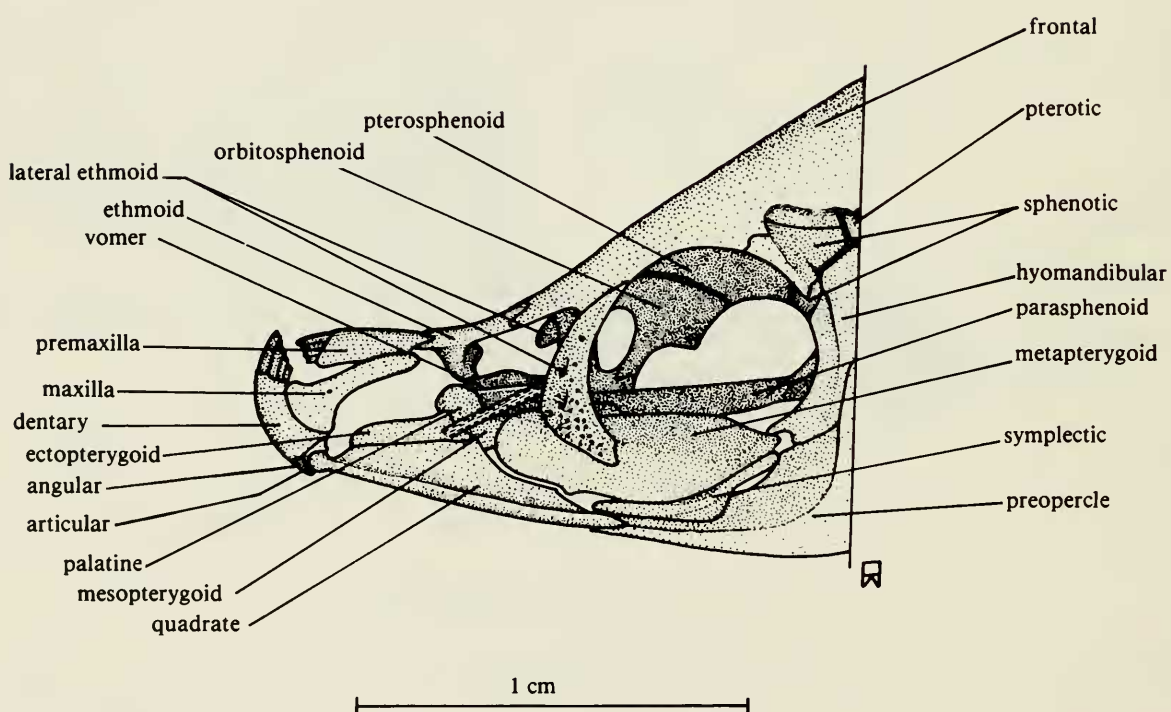


Fig. 38 *Anostomus spiloclistron*. Left lateral view of anterior region of skull (infraorbitals removed).

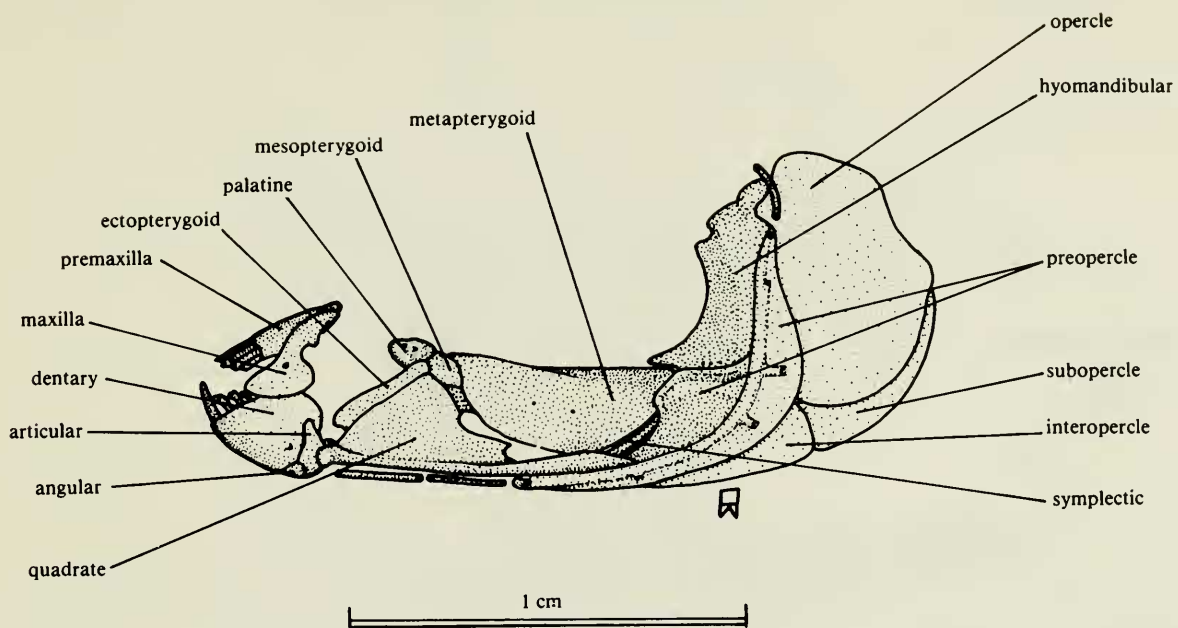


Fig. 39 *Synaptolaemus cingulatus*. Left lateral view of suspensorium and jaws.

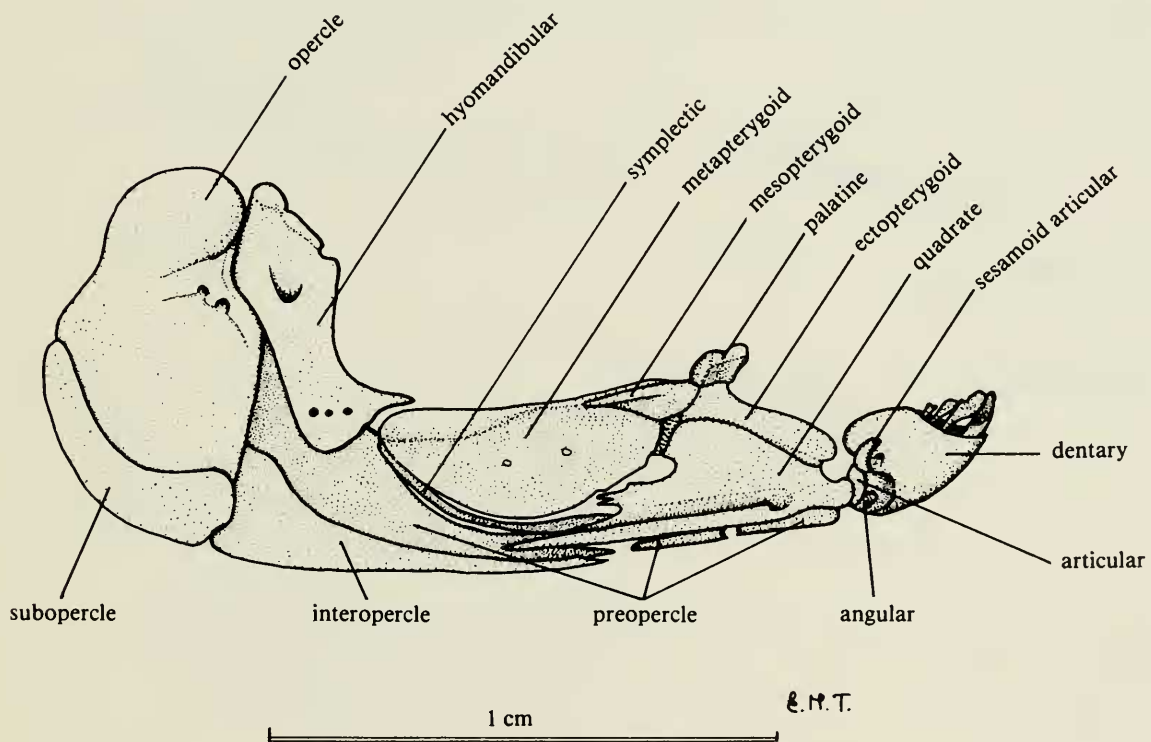


Fig. 40 *Synaptolaemus cingulatus*. Medial view of left suspensorium and lower jaw.

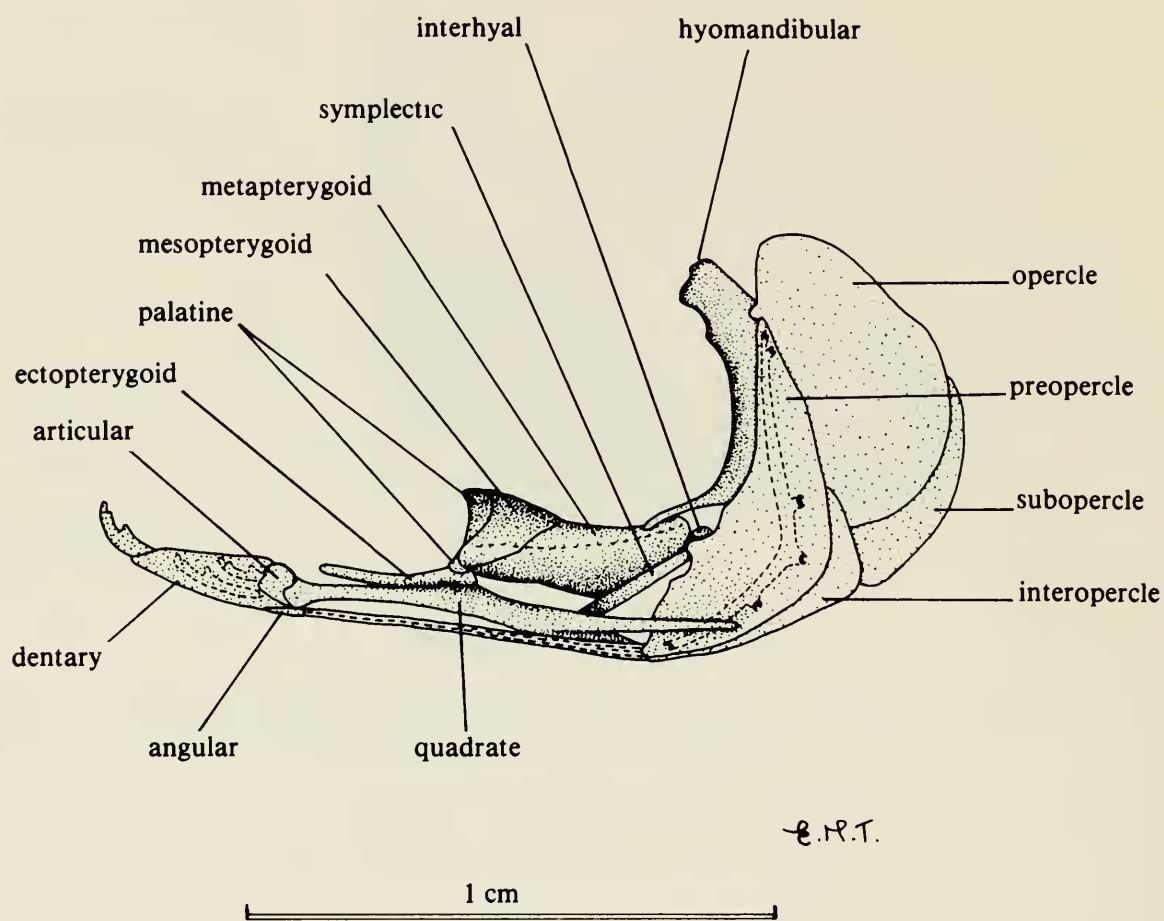


Fig. 41 *Gnathodolus* sp. Left lateral view of suspensorium and lower jaw (mirror image of right side).

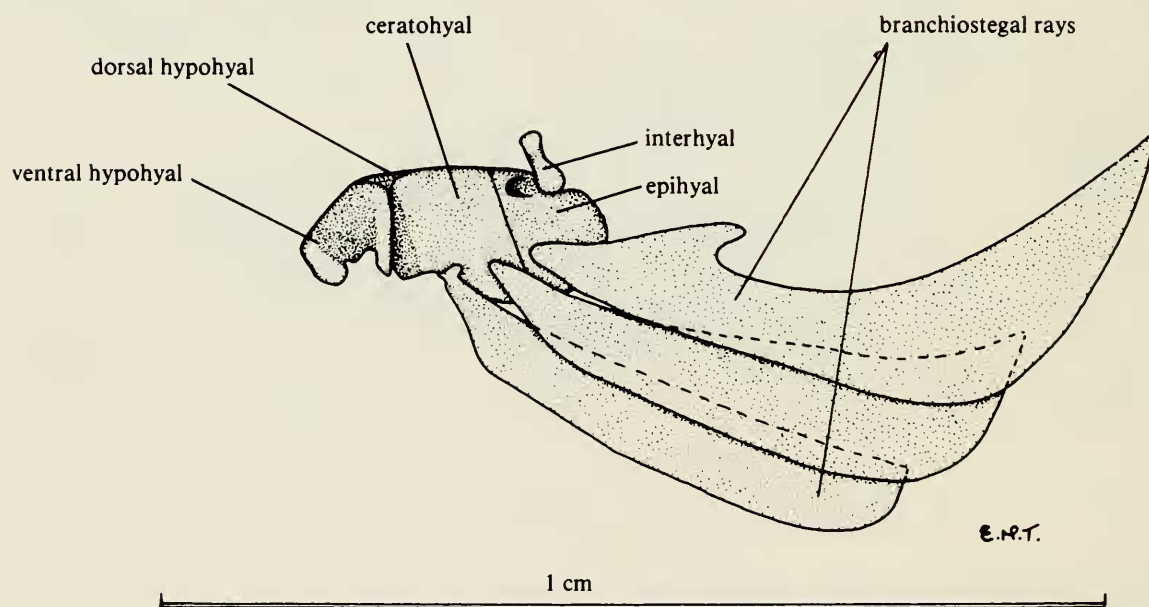


Fig. 42 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Left lateral view of hyoid arch and branchiostegal rays.

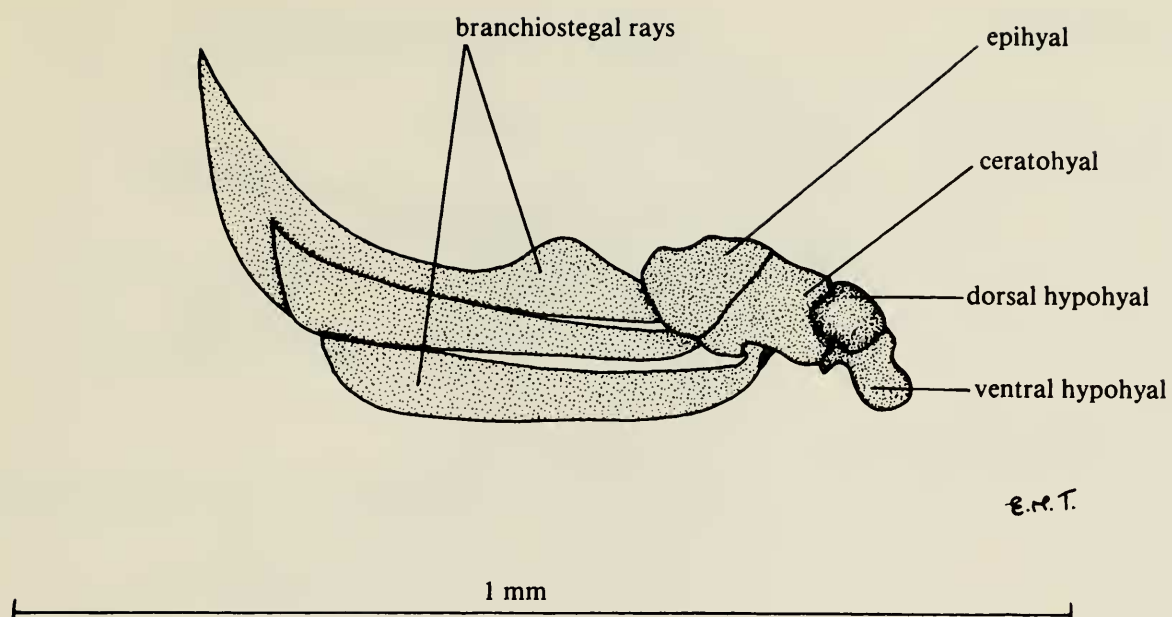


Fig. 43 *Pseudanos trimaculatus*, RUSI 5521, 52.1 mm SL. Medial view of left hyoid arch and branchiostegal rays.

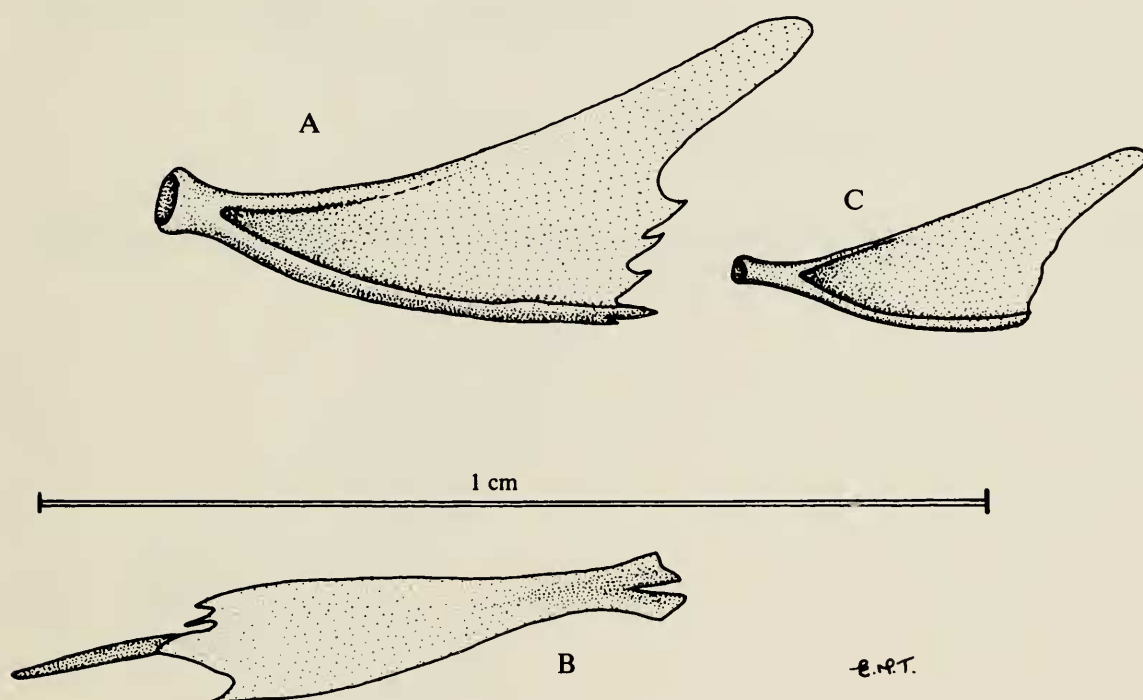


Fig. 44 Urohyal of *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL.

A Left lateral view.

B Ventral view.

C RUSI 5521, 52.1 mm SL, left lateral view.

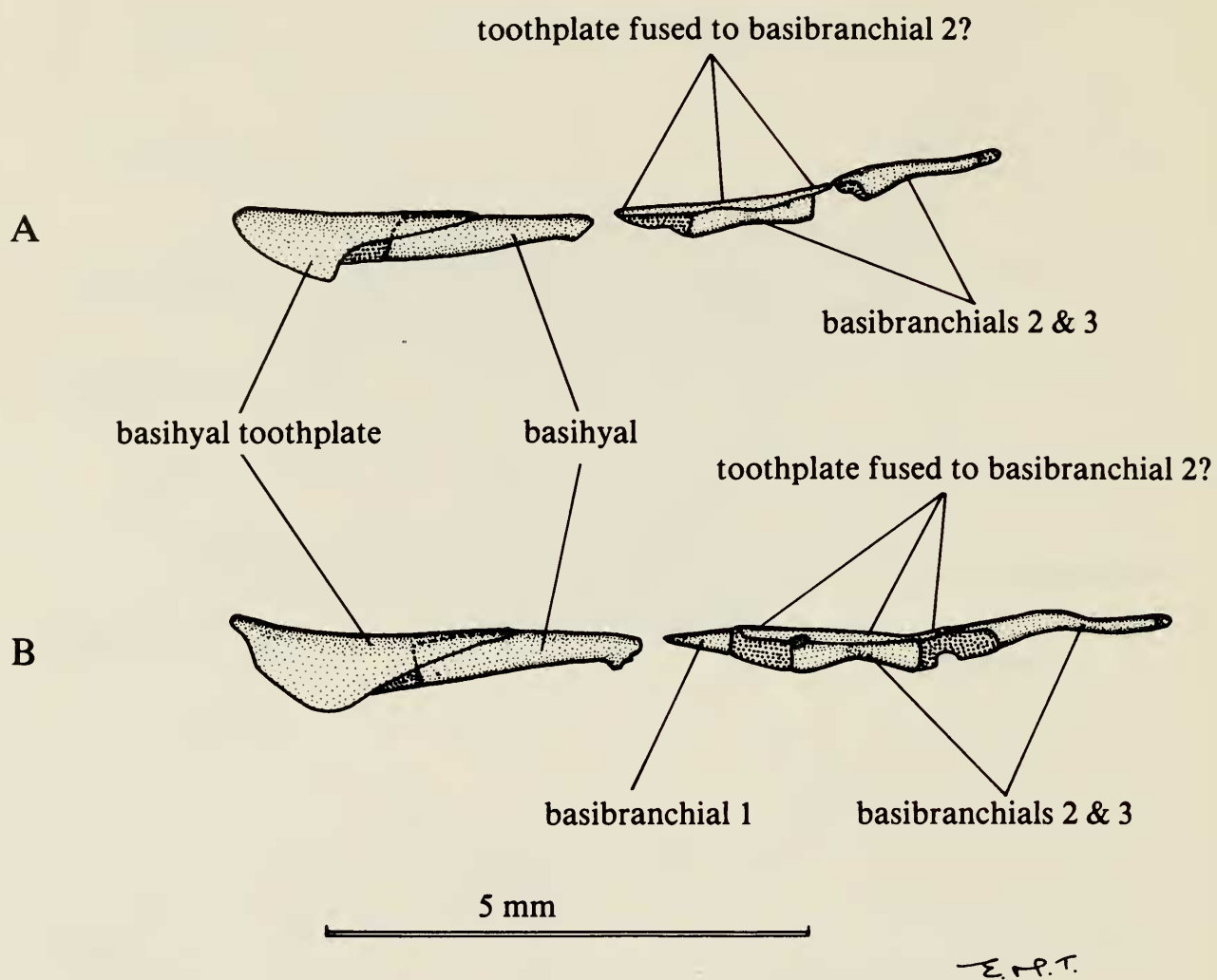
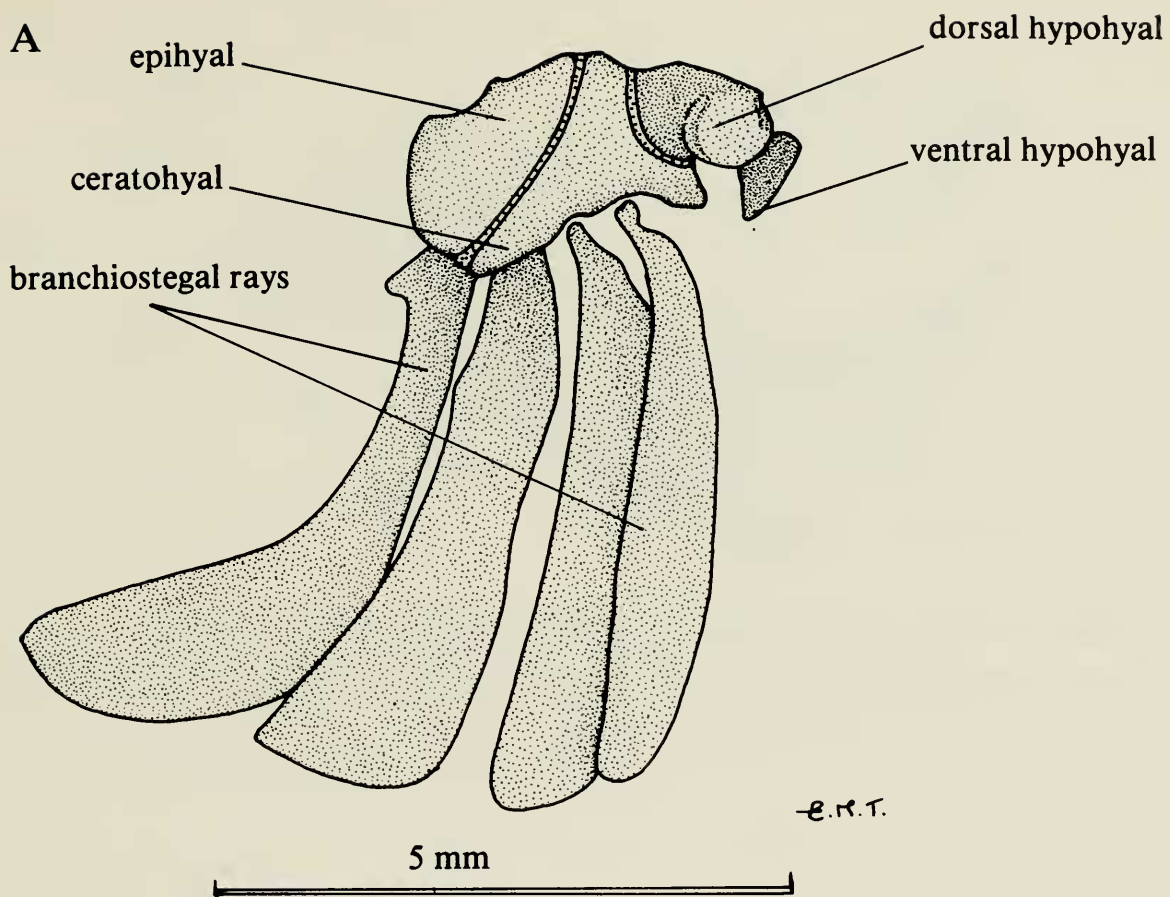


Fig. 45 A *Pseudanos irinae*, CAS 20097, 74.0 mm SL. Left lateral view of basihyal and basibranchials.
 B *P. trimaculatus*, RUSI 5521, 86.0 mm SL. As above.



B

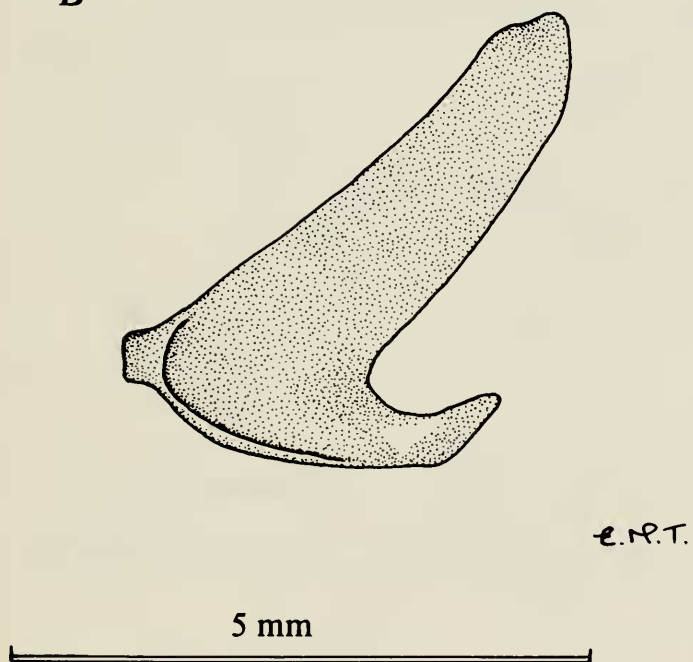


Fig. 46 *Anostomus spiloclistron*.
 A Medial view of left hyoid arch and branchiostegal rays.
 B Left lateral view of urohyal.

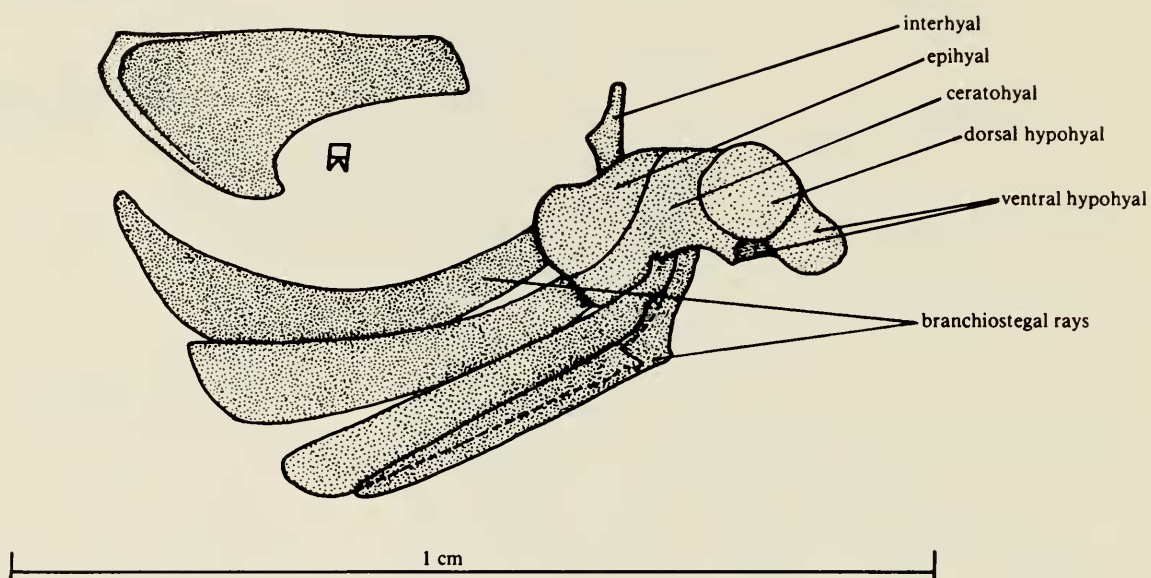


Fig. 47 *Synaptolaemus cingulatus*. Medial view of left hyoid arch and branchiostegal rays, with a left lateral view of the urohyal (above, left).

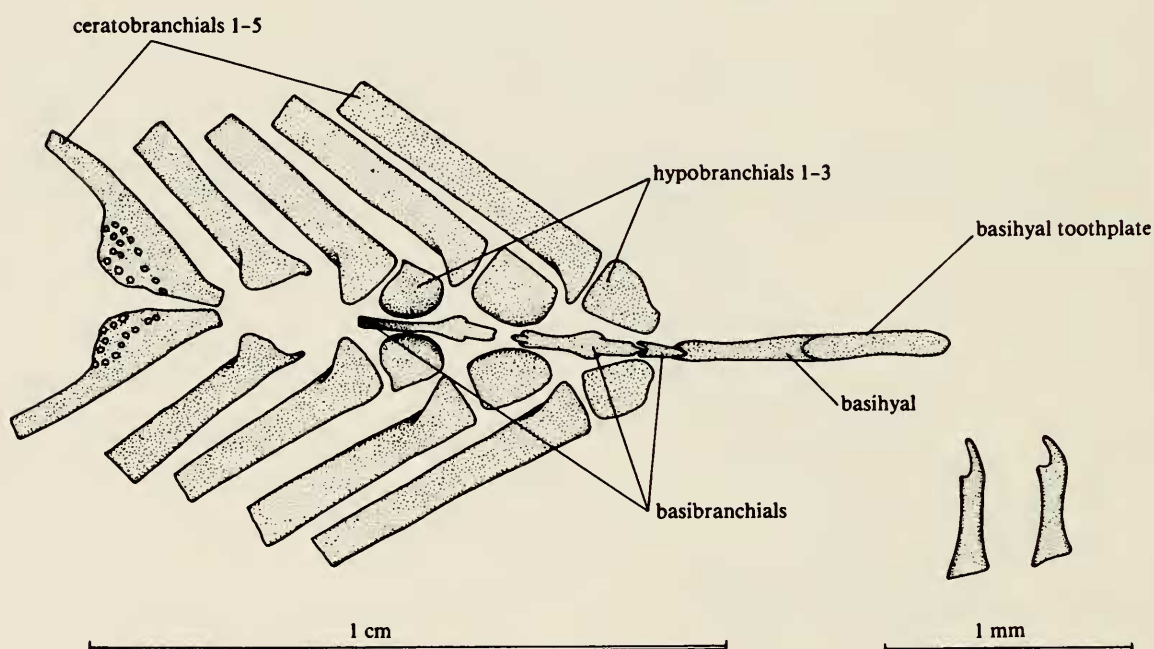


Fig. 48 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Dorsal view of ventral elements of branchial arches. Inset right: Left lateral view of two teeth from the fifth ceratobranchial toothplate.

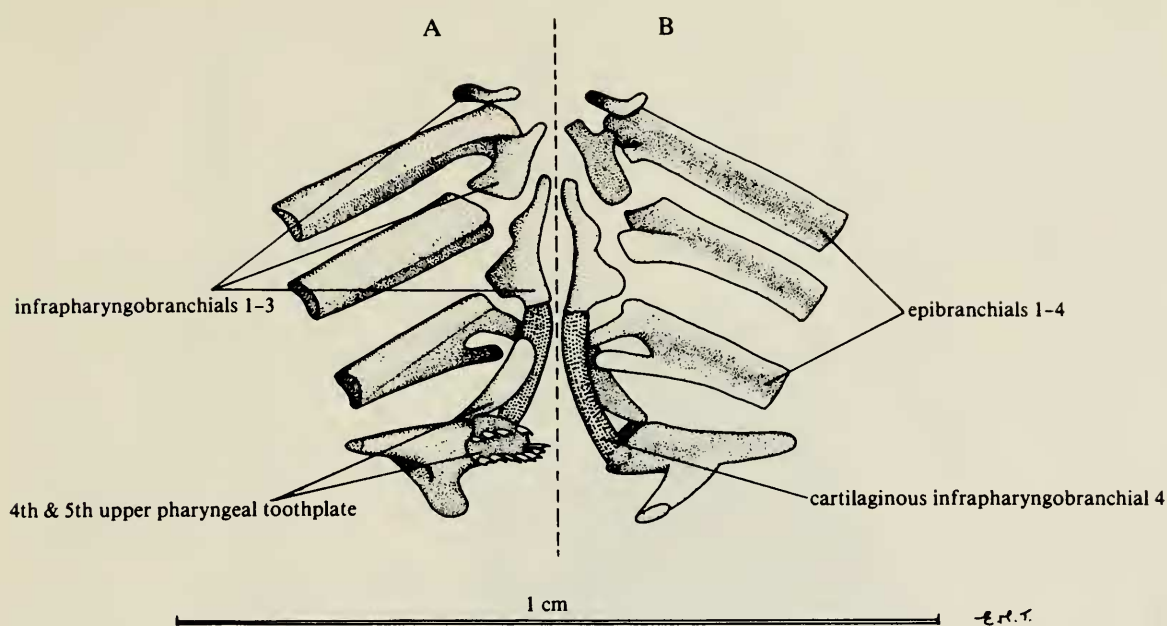


Fig. 49 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL.
 A Ventral view of dorsal elements of branchial arches.
 B Dorsal view of dorsal elements of branchial arches.

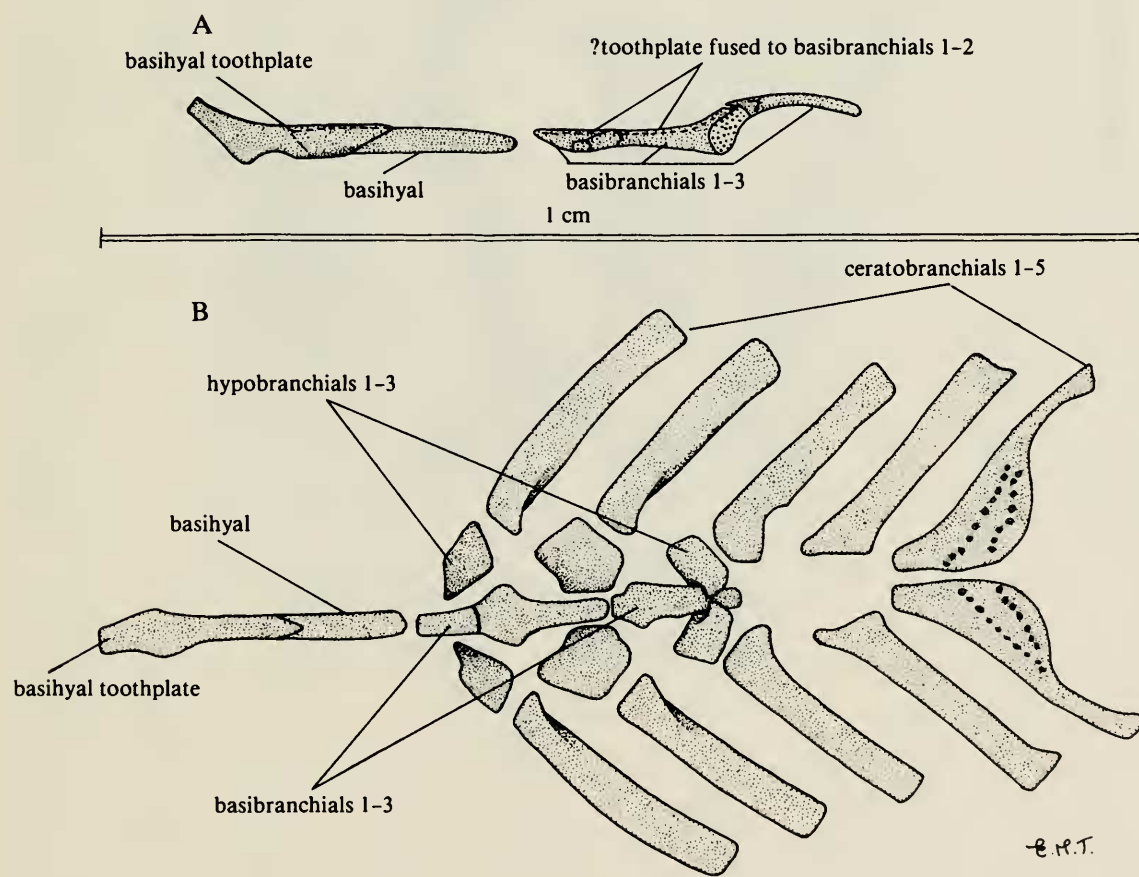


Fig. 50 *Synaptolaemus cingulatus*.
 A Left lateral view of the median elements of the hyoid and branchial arches.
 B Dorsal view of the median elements of the hyoid arch and the ventral elements of the branchial arches.

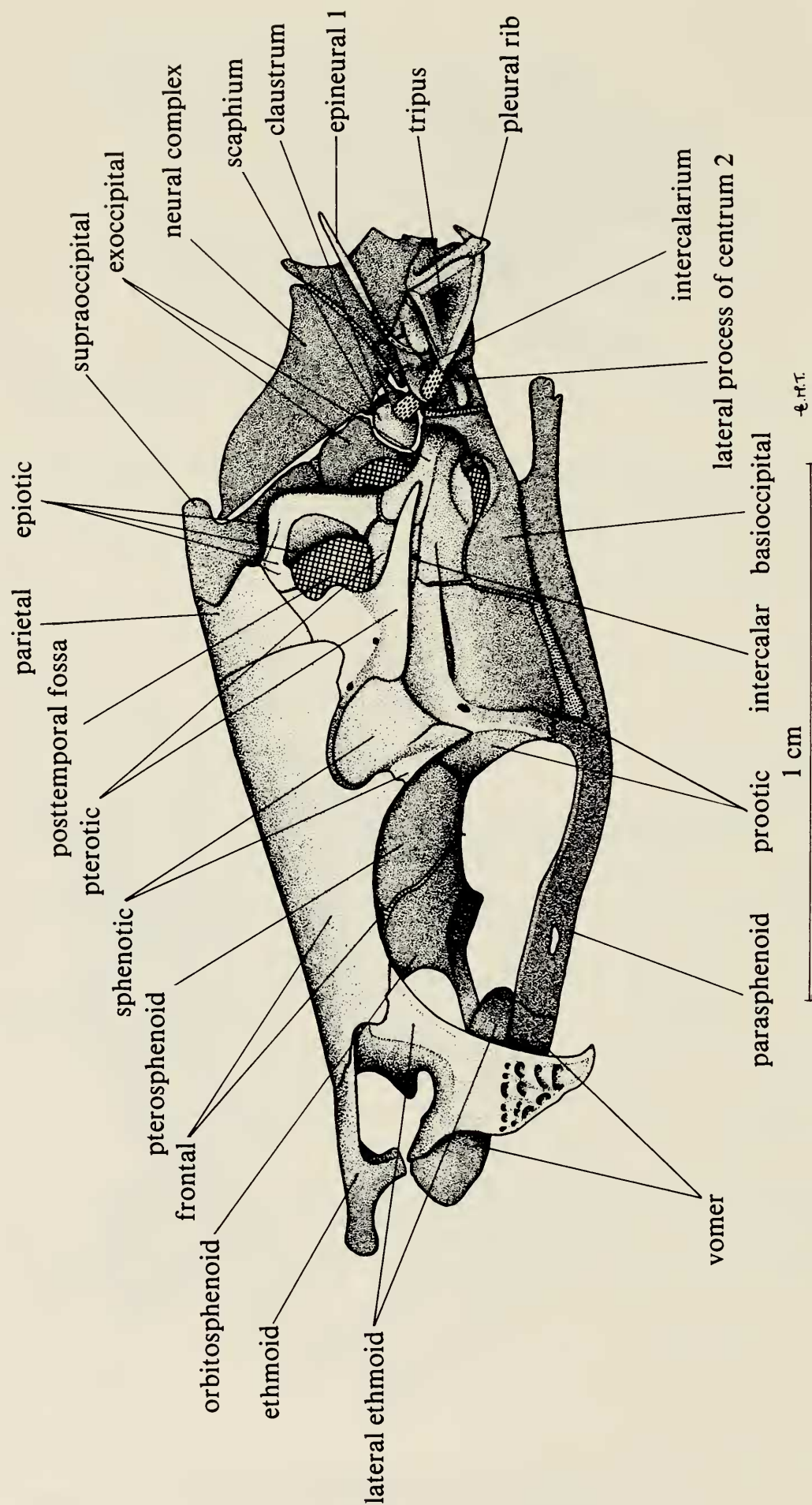


Fig. 51 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Left lateral view of cranium and Weberian apparatus.

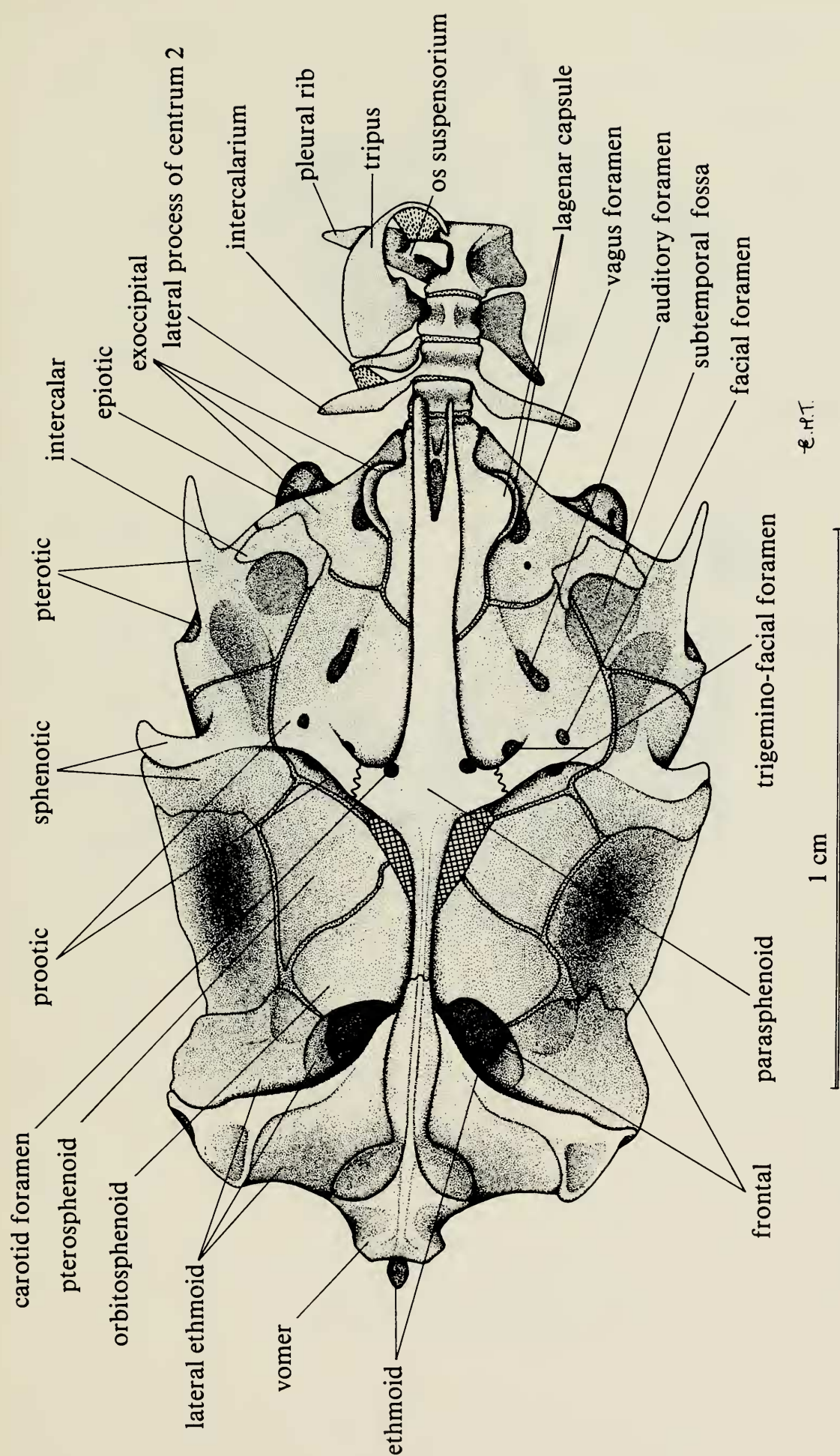


Fig. 52 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Ventral view of cranium and Weberian apparatus. Scaphium removed.

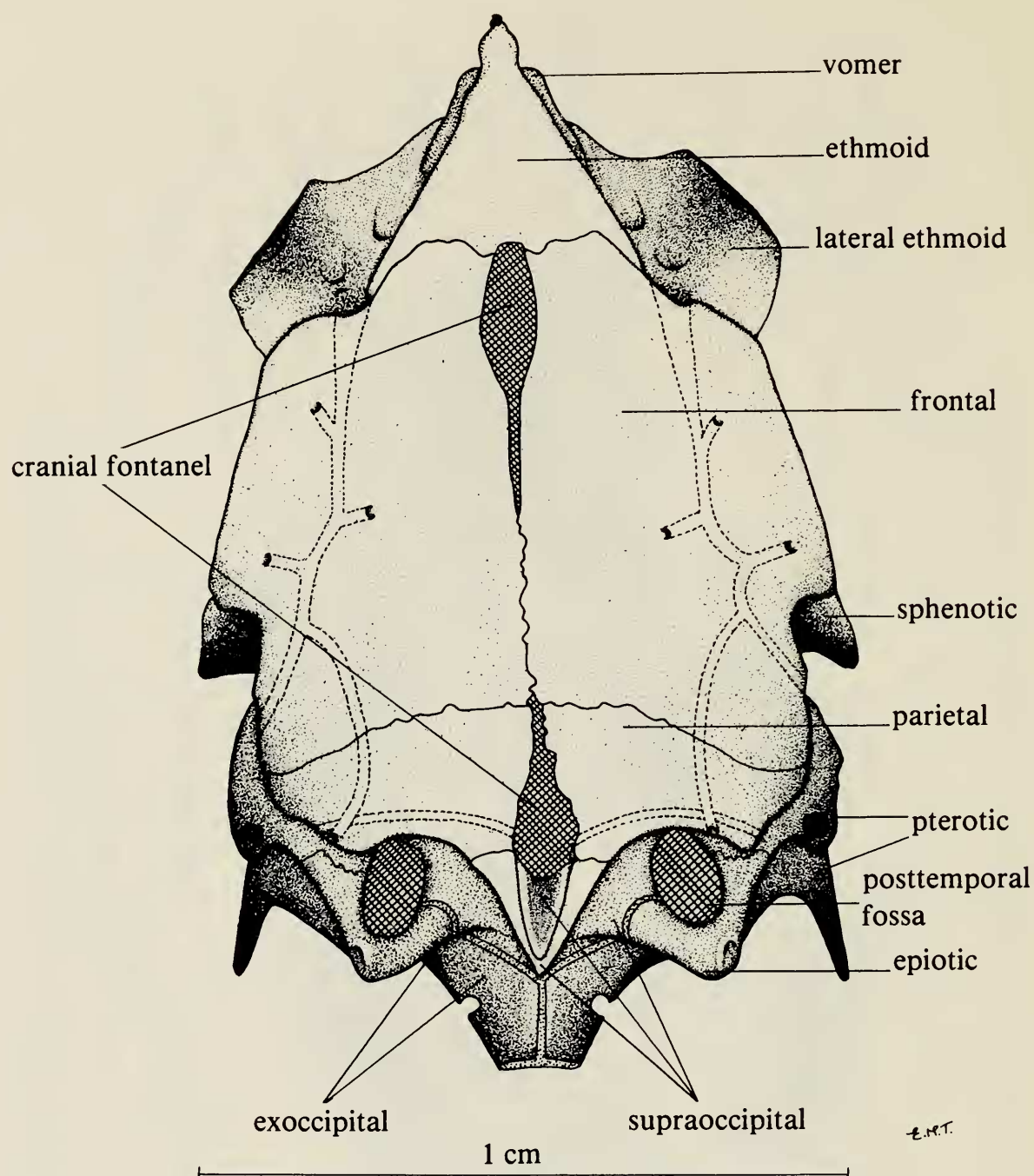


Fig. 53 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Dorsal view of cranium.

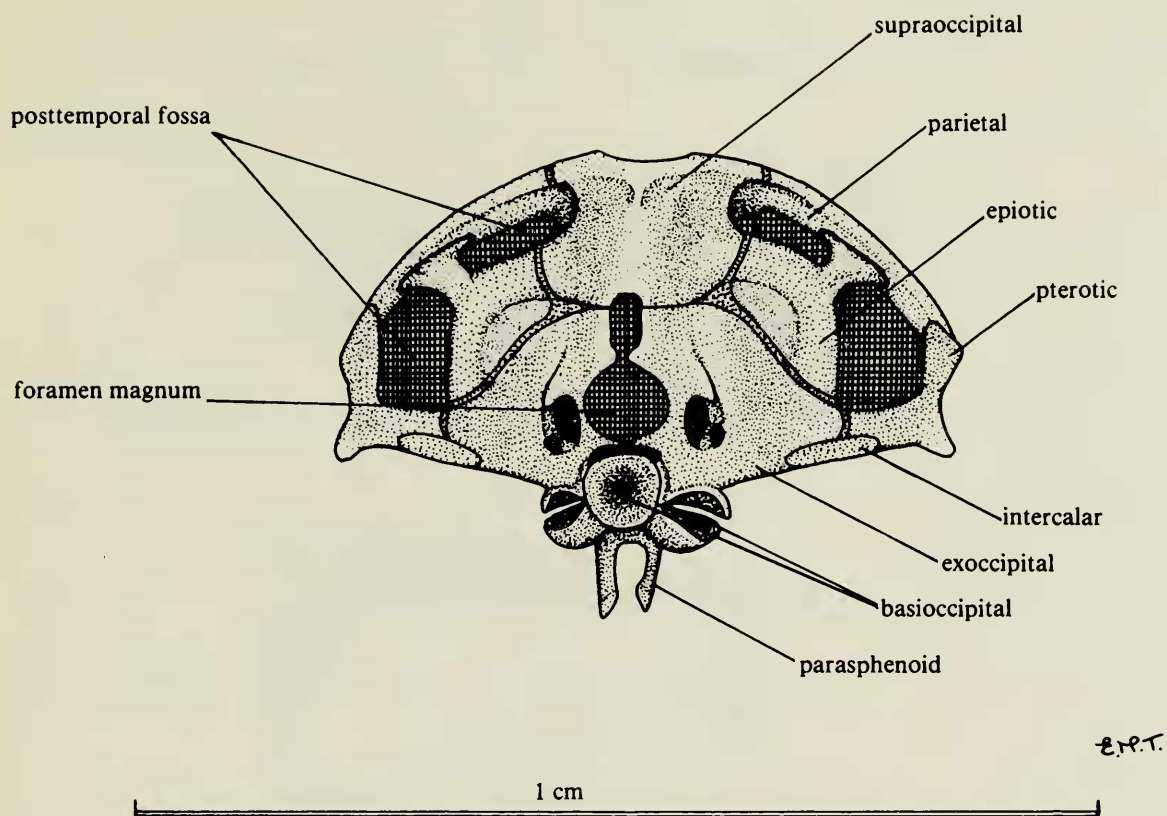


Fig. 54 *Pseudanos trimaculatus*, RUSI 5521, 52.1 mm SL. Posterior view of cranium.

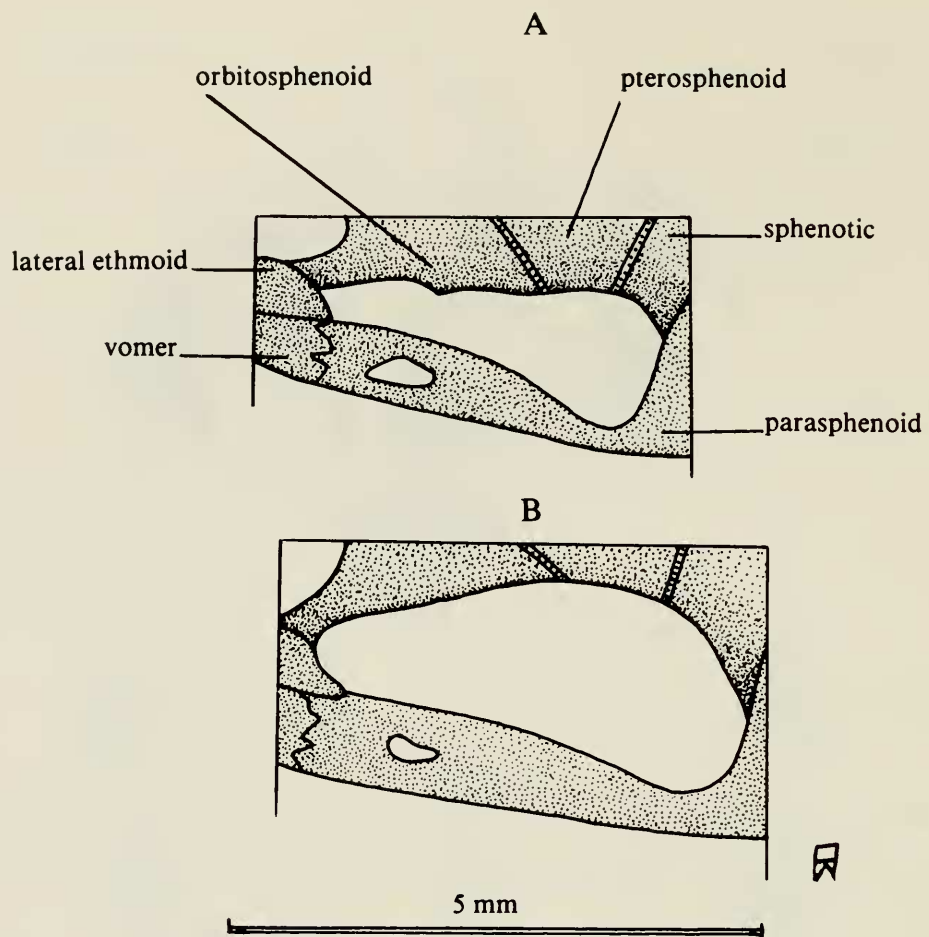


Fig. 55 *Pseudanos trimaculatus*, RUSI 5521. Left lateral view of orbit to show foramen in parasphenoid.
 A 52.1 mm SL.
 B 67.6 mm SL.

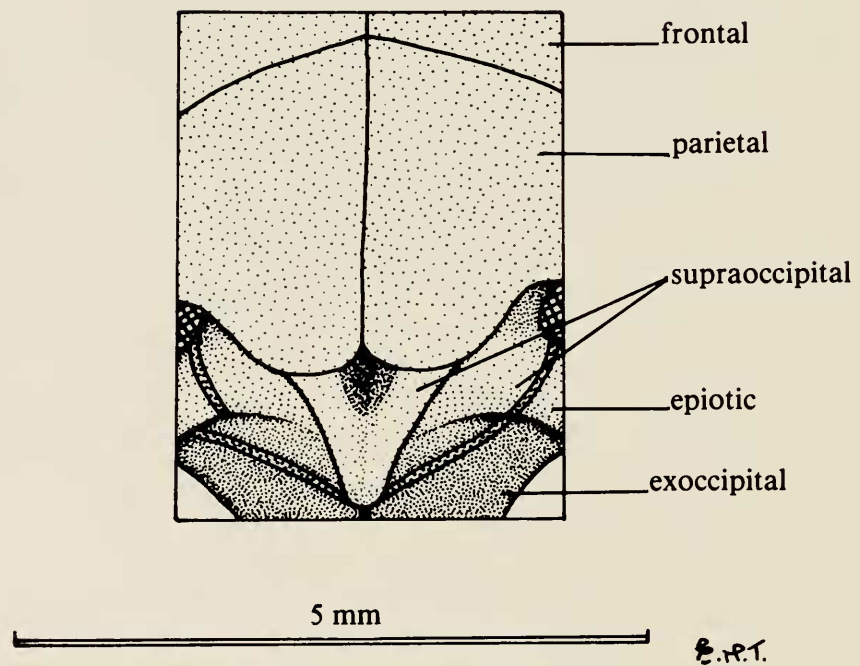


Fig. 56 *Anostomus anostomus*, RUSI 5522, 74.0 mm SL. Dorsal view of posterior region of skull.

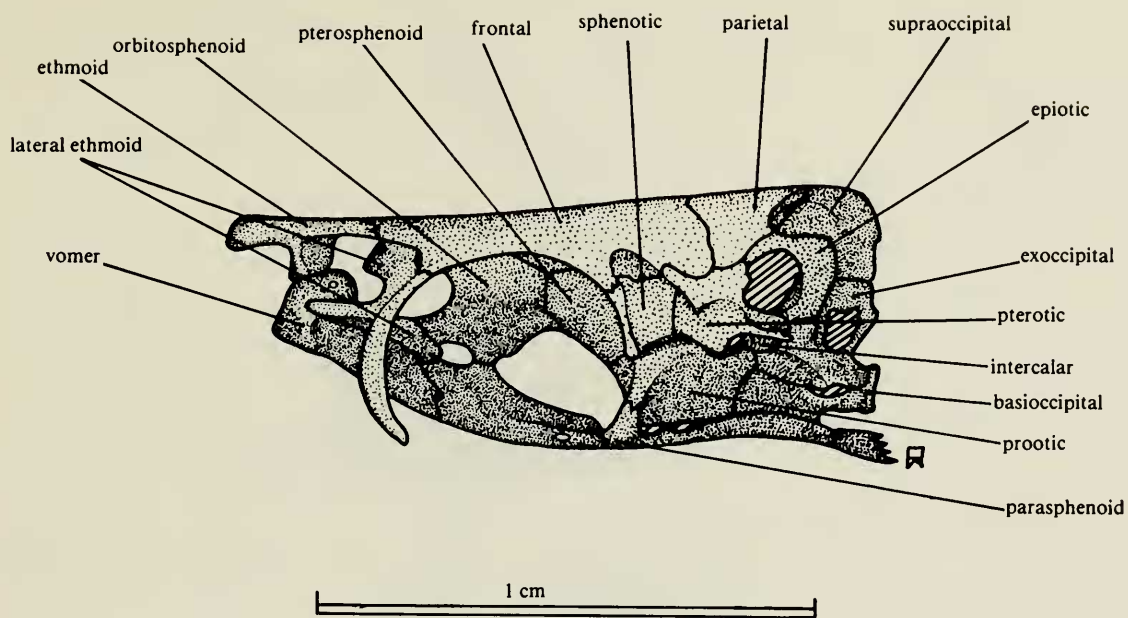


Fig. 57 *Synaptolaemus cingulatus*. Left lateral view of cranium.

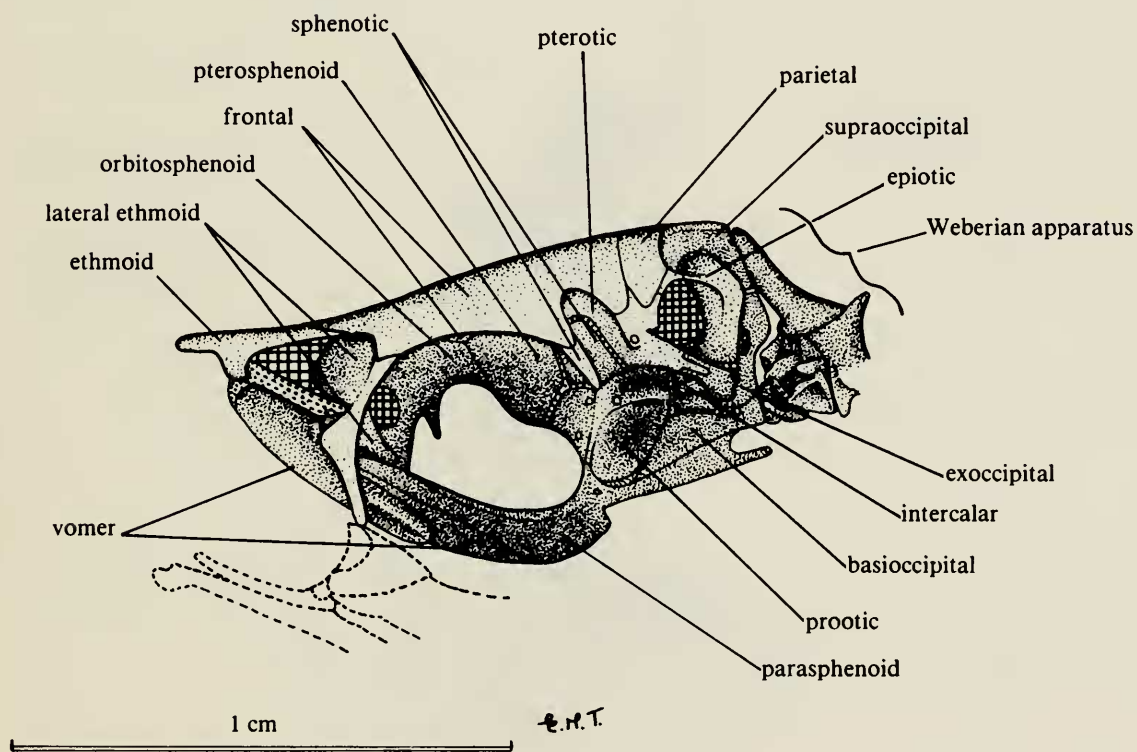


Fig. 58 *Gnathodolus* sp. Left lateral view of cranium (mirror image of right side). Anterodorsal portion of suspensorium (see Fig. 41) in dashed outline to show its articulation point with the vomer.

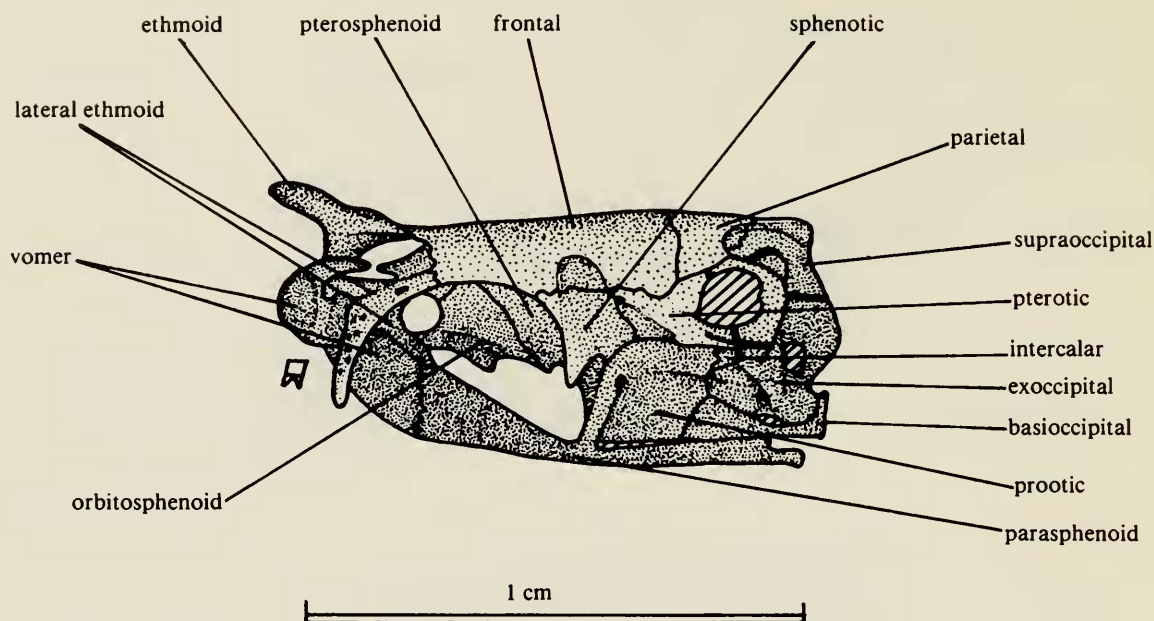


Fig. 59 *Sartor respectus*. Left lateral view of cranium.

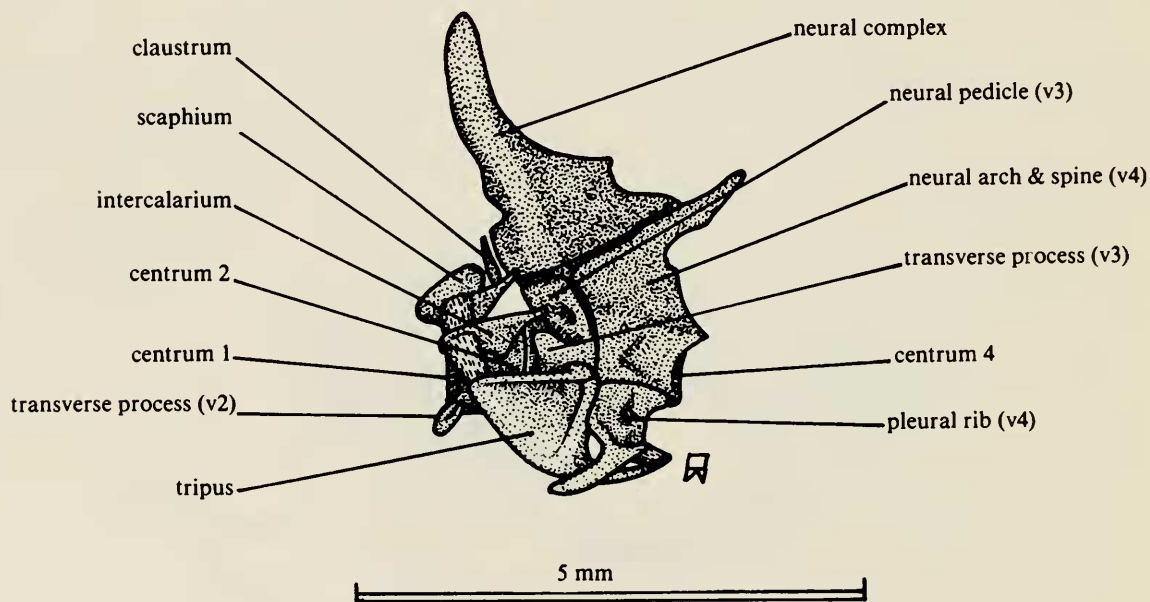


Fig. 60 *Synaptolaemus cingulatus*. Left lateral view of Weberian apparatus.

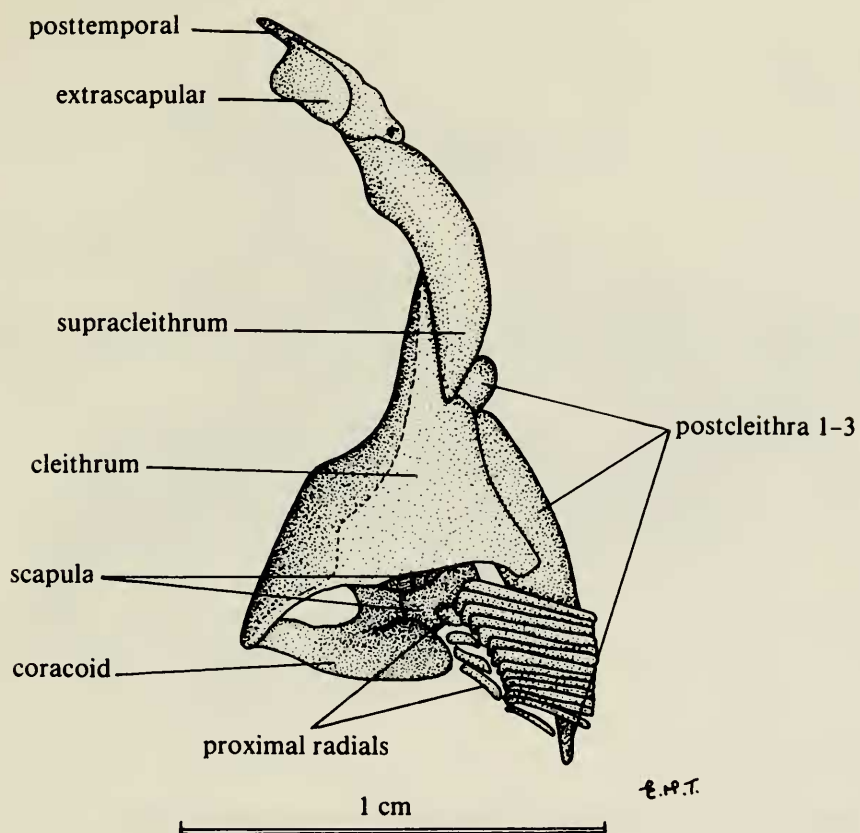


Fig. 61 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Lateral view of left pectoral girdle.

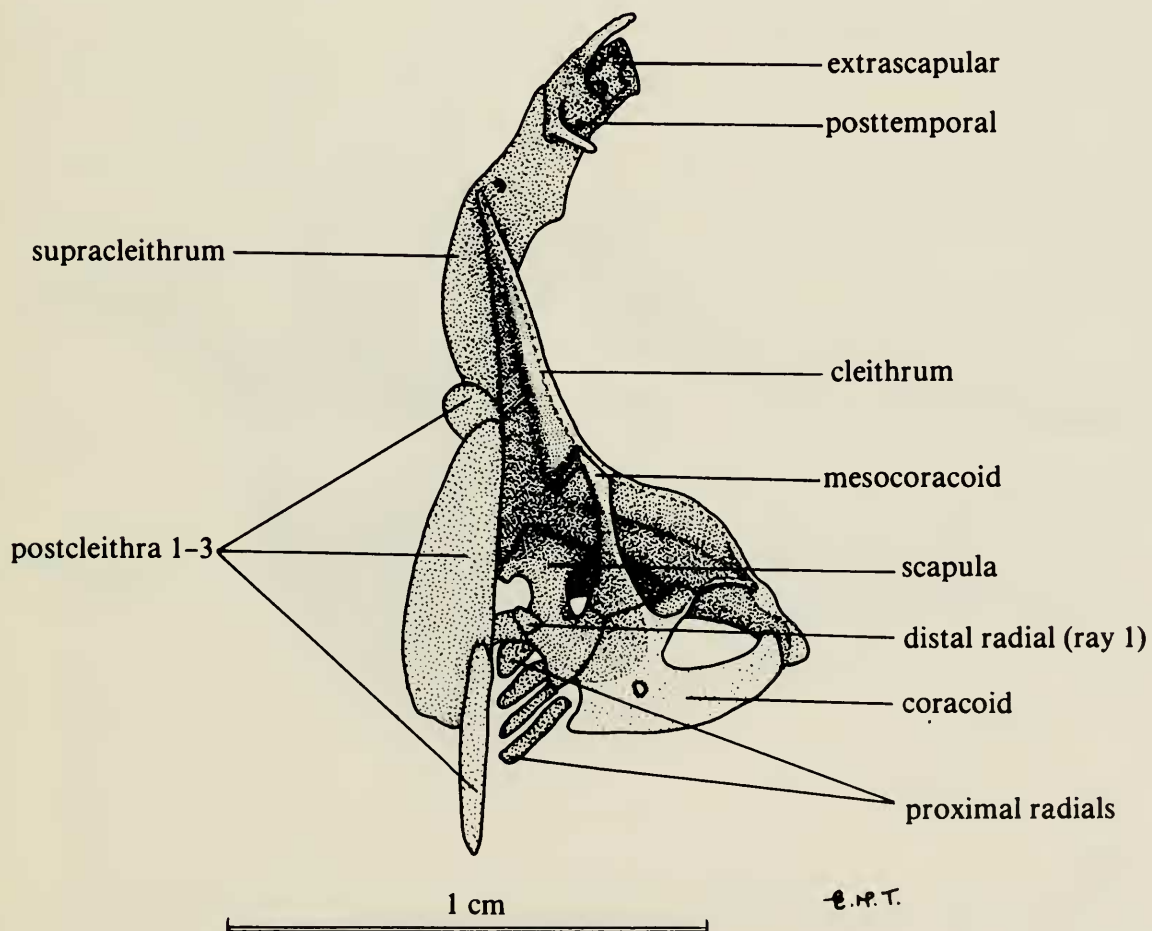


Fig. 62 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Medial view of left pectoral girdle.

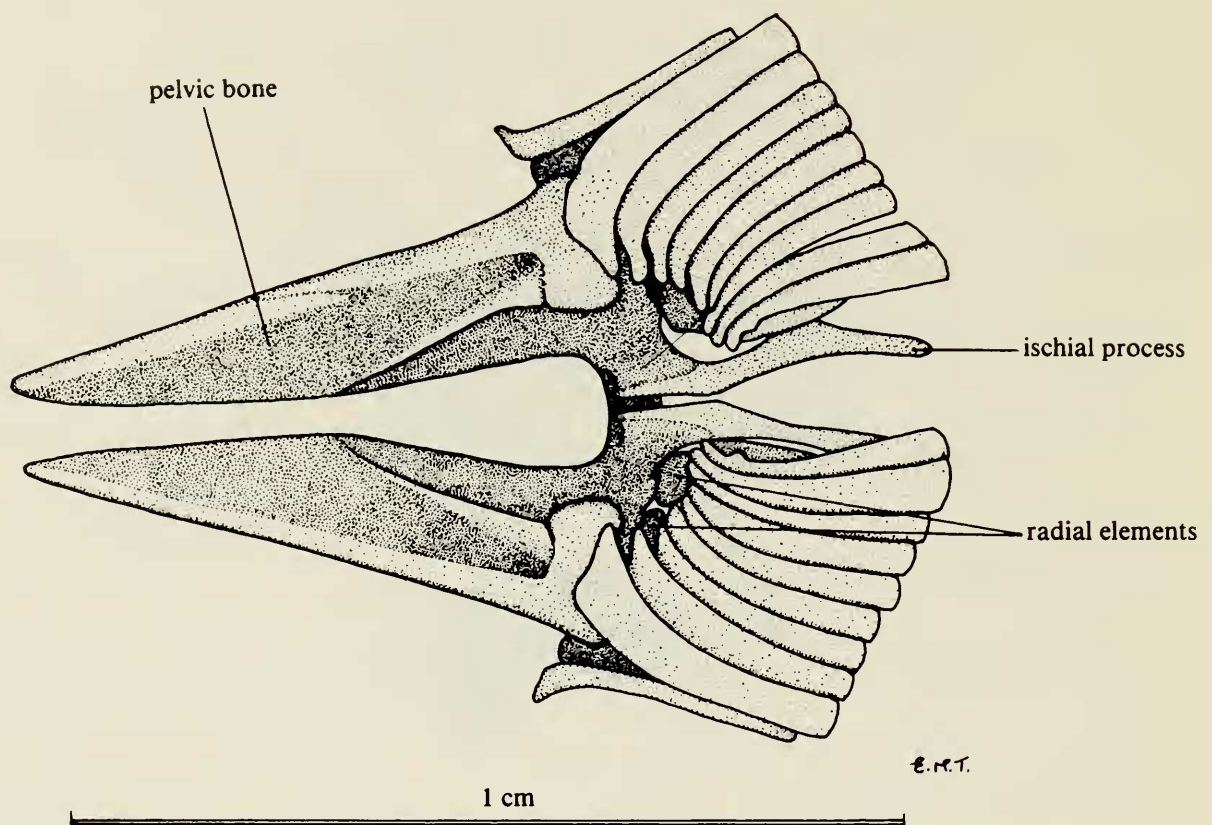


Fig. 63 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Ventral view of pelvic girdle and fins.

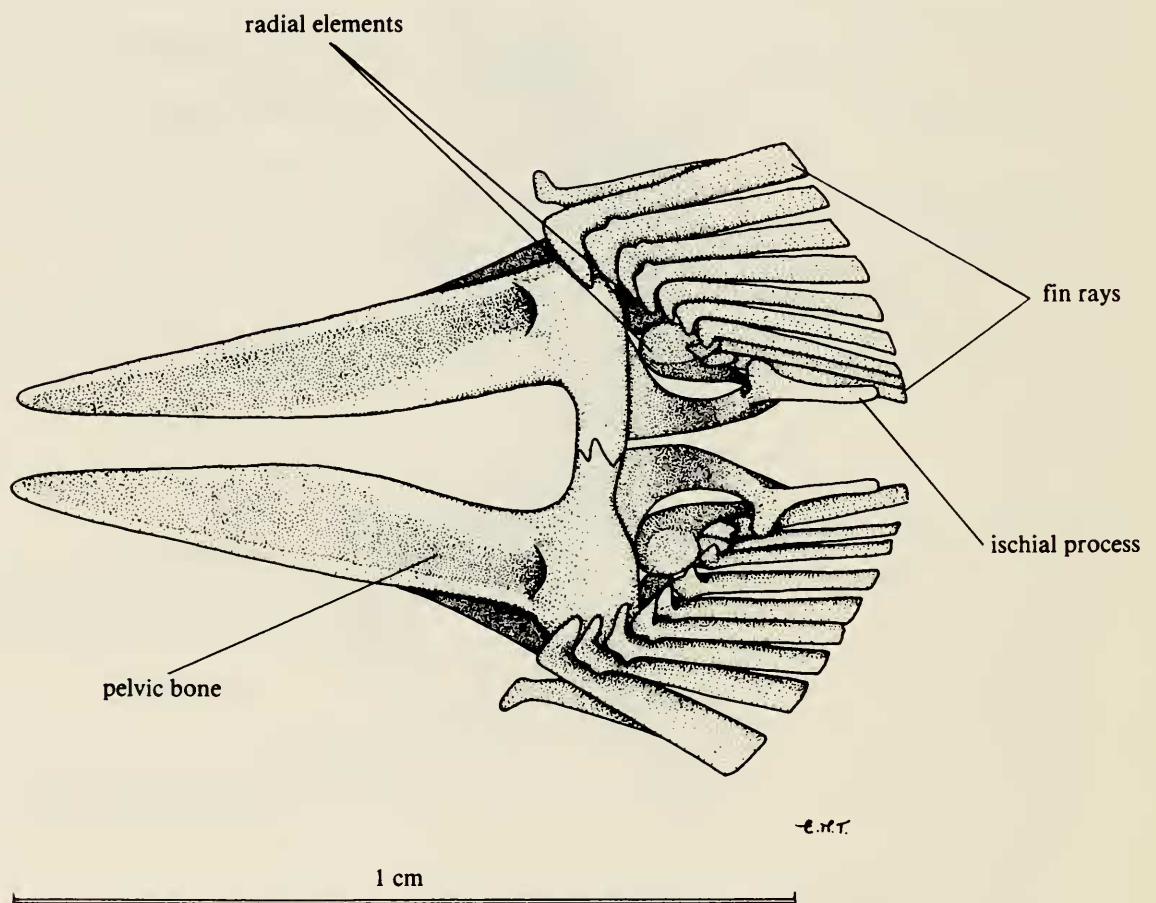


Fig. 64 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Dorsal view of pelvic girdle and fins.

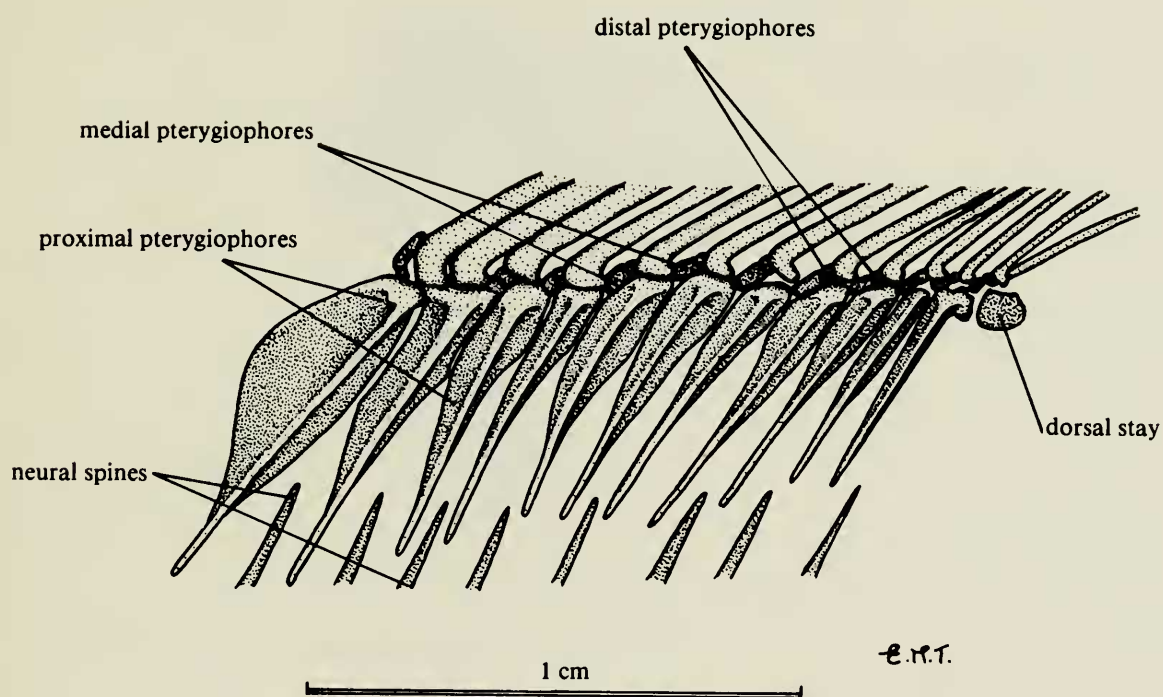


Fig. 65 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Left lateral view of dorsal fin and supporting elements.

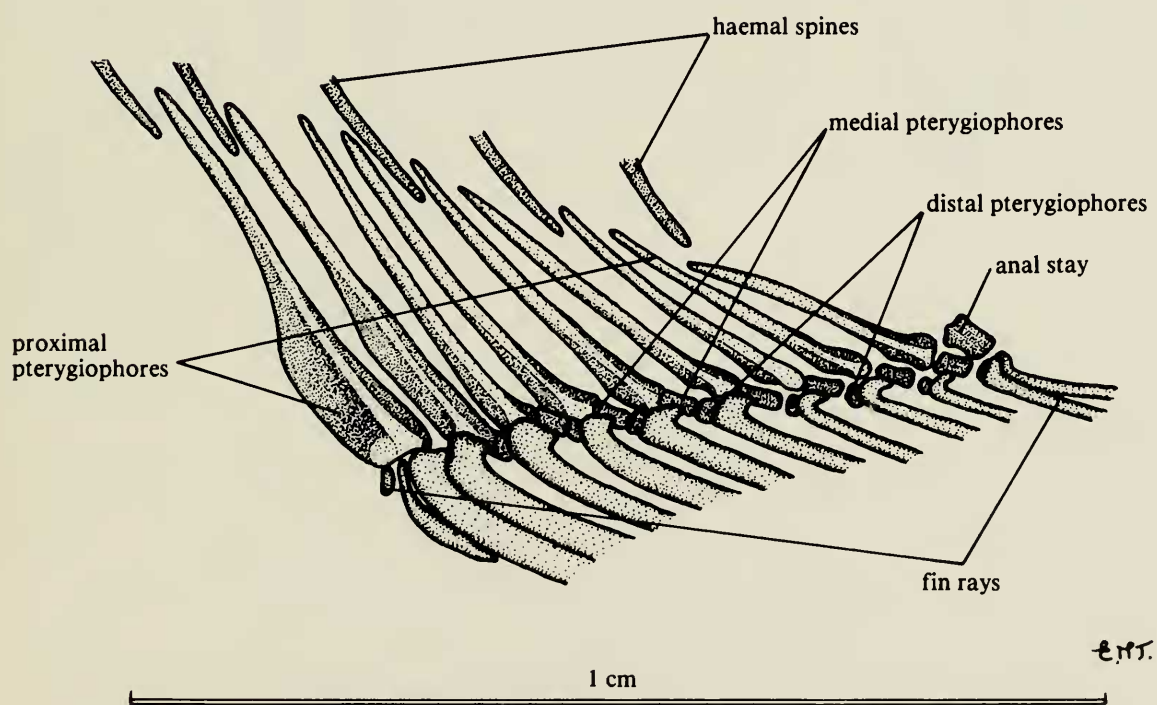


Fig. 66 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Left lateral view of anal fin and supporting elements.

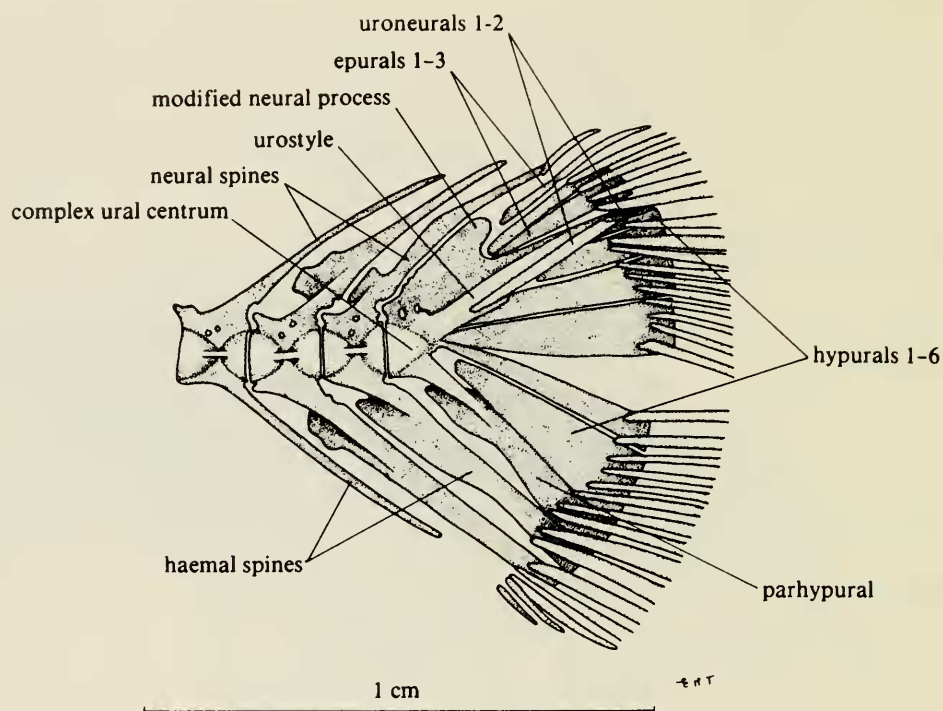


Fig. 67 *Pseudanos trimaculatus*, RUSI 5521, 86.0 mm SL. Left lateral view of caudal skeleton.

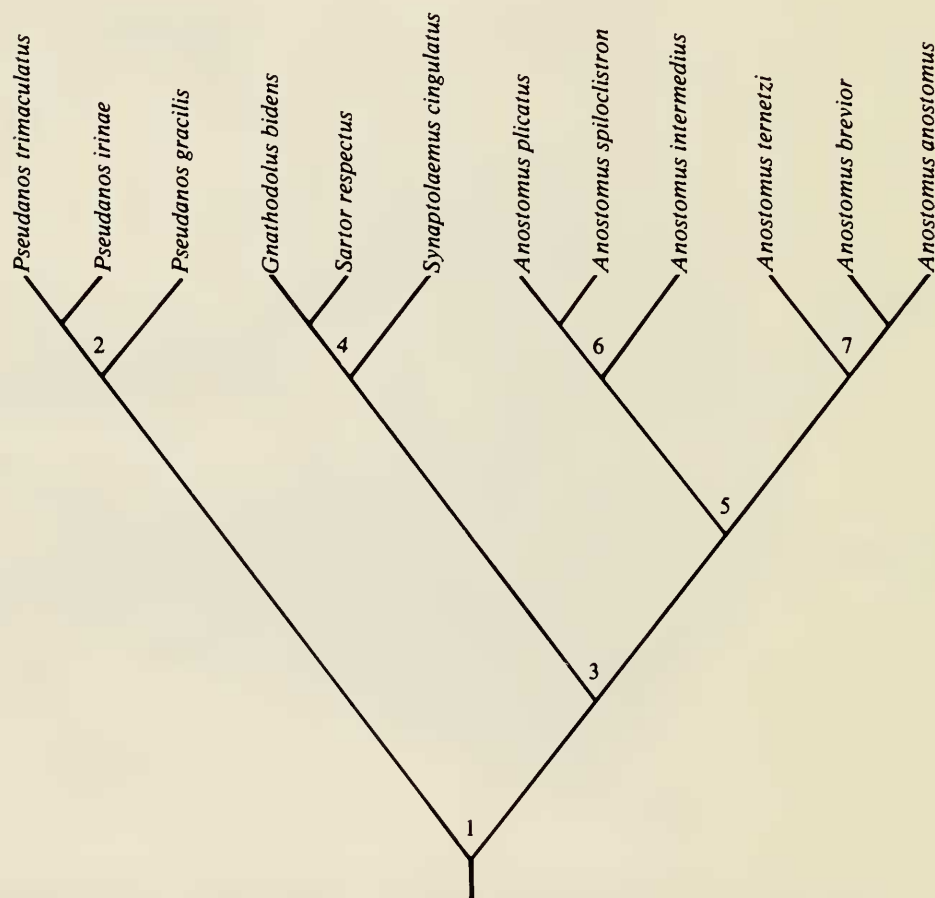


Fig. 68 Hypothesized phylogeny of the Anostominae. Numbers at the base of each dichotomy refer to the branch points so numbered in the Discussion section of this paper.